



















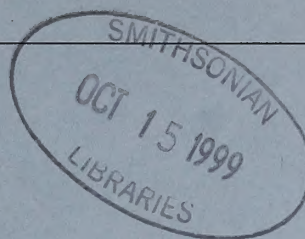


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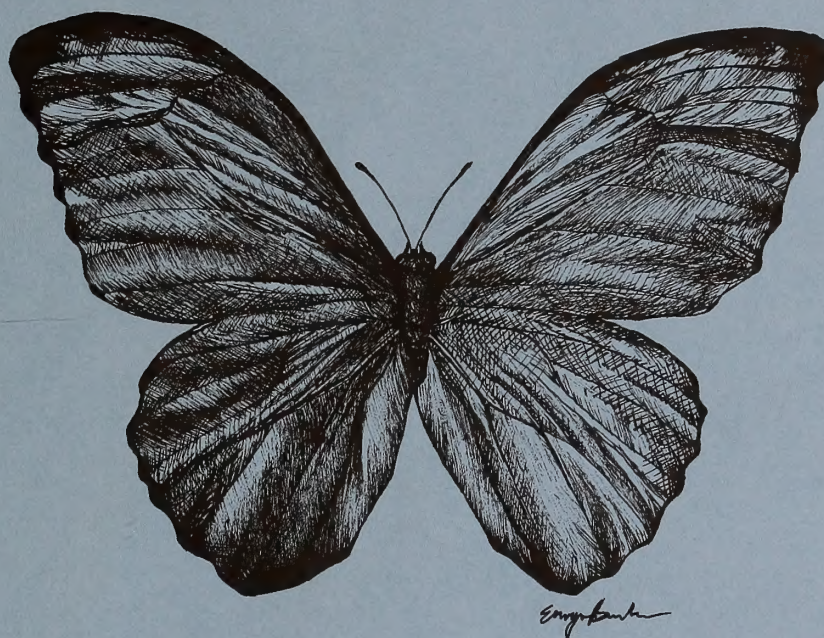
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**Cover illustration:** Pen and ink illustration by Eowyn Burke of *Morpho menelaus* (Nymphalidae: Morphinae). Specimen was from the insect collection of the Entomology Section of the University of Colorado Museum, Boulder, CO. No data were associated with the specimen.



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## CONTRIBUTION TOWARDS THE STUDY OF THE PYRALINAE (PYRALIDAE): HISTORICAL REVIEW, MORPHOLOGY, AND NOMENCLATURE

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**ABSTRACT.** The monophyly of the Pyralinae and the two tribes, Pyralini and Endotrichini, is reviewed based on an analysis of previously used morphological characters of the adult and larva. Characters previously used to define these groups are plesiomorphic (i.e., they are not valid) or highly homoplastic (i.e., they are not reliable) to support the taxa as monophyletic, or both. We describe the male genitalia and present characters to support the monophyly of the Endotrichini, but the Pyralini is likely a paraphyletic taxon. Larval characters did not provide evidence to support or reject monophyly for either group. Based on male genitalic morphology we reassign genera, and make additions or changes within these taxa in recently published checklists. In the Neotropical fauna: *Perforadix* Sein is transferred to the Pyraustinae and is a **new synonym** of *Sufetula* Walker; a lectotype is designated for *Perforadix sacchari* Sein; *Micronix* Amsel is transferred from the Pyralinae to the Crambinae; and *Micromastra* Schaus and *Taboga* Dyar, revised status, remain in the Pyralinae. In addition, *Sufetula pygmaea* Hampson, presently in the Crambidae, is transferred to the Noctuidae: *Nola pygmaea* Hampson (Nolinae), **new combination**. In the Australian fauna *Macna* Walker is transferred from the Pyralinae to the Chrysauginae. A list of the subfamilies and tribes of the Pyralidae worldwide and of the species of the Pyralini of the Western Hemisphere are included.

**Additional key words:** Endotrichini, Pyralini, Neotropics, Australia, larval morphology.

Within the Pyraloidea, the Pyralinae are a large group of about 900 species that are more diverse in Africa and Asia than in the Western Hemisphere. This subfamily includes the worldwide stored-product pest species *Pyralis farinalis* Linnaeus, also known as the meal moth. A complete study to investigate the monophyly of the Pyralinae has never been conducted. However, Solis and Mitter (1992) proposed a character to define the Pyralinae and hypothesized it to be the sister group to the phycitine + epipaschiine clade (Table 1). In this paper we integrate previous findings in the Pyralinae and our observations to facilitate future studies on these moths.

Presently, there are two tribes in the Pyralinae, the Endotrichini and Pyralini (Table 1). The Endotrichini includes 7 genera, *Endotricha* Zeller being the largest genus with about 70 species. Based on our morphological and label data observations, the tribe is distributed

only in Asia and Africa. The Pyralini include 118 genera, with the vast majority of the species distributed in Africa and Asia, although some occur worldwide. The two tribes have been defined by two states of a hindwing venational character (Endotrichini = Rs anastomosed with Sc+R<sub>1</sub>; Pyralini = Rs not anastomosed with Sc+R<sub>1</sub>) and they have been shifted between tribal and subfamilial rank based on the importance placed on this character by various authors (e.g., Ragonot 1891, Hampson 1896, Whalley 1961, Minet 1982). We dispute the validity of the use of the hindwing venational character at suprageneric levels. We also explore the literature and investigate the morphology of larval stage as an independent character set.

Recent publication of two checklists (Shaffer et al. 1996, Shaffer & Solis 1995) of the Pyralini and Endotrichini of Australia and the Neotropics, and the previous publication of the checklist of the Pyraloidea



TABLE 1. Higher classification of the Pyralidae; current tribal names in use, although most tribes have not been shown to be monophyletic.

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Pyralidae Latreille
<b>Chrysauginae</b> Lederer
<b>Galleriinae</b> Zeller
<b>Galleriini</b>
<b>Megarhtridiini</b>
<b>Tirathabini</b>
<b>Cacotherapiini</b>
<b>Pyralinae</b> Latreille
<b>Pyralini</b>
<b>Endotrichini</b>
<b>Epipaschiinae</b> Meyrick
<b>Phycitinae</b> Zeller
<b>Cryptoblabini</b>
<b>Phycitini</b>
<b>Cabiniini</b>
<b>Anerastiini</b>
<b>Peoriini</b>

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of North America north of Mexico (Munroe 1983) have laid the groundwork for studies on the systematics of the Pyraloidea. A large number of taxon transfers, and even misplaced taxa between superfamilies, have been documented in the recently published checklists. We herein explain how assignments in recent Australian (Shaffer et al. 1996) and Neotropical (Shaffer & Solis 1995) checklists were made based on our observations on male genitalic morphology and larval morphology. We also list corrections to the tribal and subfamilial headings of the recently published checklists, and list additions or changes made since their publication.

#### MATERIALS AND METHODS

The collections at The Natural History Museum (BMNH), London, England; the National Museum of Natural History (USNM), Washington, D.C., USA; the Cornell University Collection (CU), Ithaca, New York, USA; and Zoologische Staatssammlung (ZSBS), Munich, Germany were studied to determine taxa not included in recently published checklists. Type specimens were examined and dissected when necessary. If the type specimen could not be located, the original descriptions and genitalic illustrations were used to place the species generically. Genitalia slides of non-type specimens were prepared, studied, and compared when type specimens were not available, or when type specimens were not in suitable condition for study.

Larvae from alcohol collections of the USNM and BMNH of *Endotricha flammealis* (Denis & Schiffermüller), *Pyralis farinalis* Linnaeus, *Aglossa caprealis* Hübner, and *Herculia psammioxantha* Dyar were examined with a stereomicroscope to verify the literature on larval morphology.

Adult and larval characters of the other subfamilies of the Pyralidae, Chrysauginae, Galleriinae, Phycitinae, Epipaschiinae, were used for outgroup comparison purposes based on a phylogenetic analysis by Solis and Mitter (1992) (Table 1).

#### HISTORICAL REVIEW AND ANALYSIS OF PREVIOUSLY USED CHARACTERS

Meyrick (1890) first brought the character of the veins 7 [=Rs] and 8 [=Sc+R<sub>1</sub>] in the hindwing to attention, and since Ragonot (1891) the Pyralini and Endotrichini have been separated and defined primarily by two character states of the hindwing venation: in the Pyralini Rs and Sc+R<sub>1</sub> approach each other (Fig. 5), but do not anastomose; in the Endotrichini the two veins anastomose for at least part of their length (Fig. 6). We propose that this character is not reliable in the separation or definition of taxa at suprageneric levels in the Pyralinae and in the following historical review we use italics to draw attention to these two character states in descriptions.

Meyrick (1890) included *Endotricha* in the Pyralinae. He included the Pyralinae and Epipaschiinae in the Pyralididae and did not recognize them as separate subfamilies. Meyrick defined (and spelled) the Pyralididae as follows:

"Ocelli present, often concealed by scales. Tongue well-developed, or sometimes obsolete. Maxillary palpi well-developed, or rarely rudimentary. Fore wings with vein 1 usually shortly or obscurely furcate at base, sometimes simple, 4 and 5 closely approximated at base or often stalked, 7 and 8 out of 9. Hind wings without defined pecten of hairs on lower margin of cell, veins 4 and 5 closely approximated at base or from a point or stalked, 7 [=Rs] out of 6 near origin or rarely separate but closely approximated, free or sometimes anastomosing with 8 [=Sc+R<sub>1</sub>]" (Meyrick 1890:433) [italics ours].

He used head and wing venational characters occurring in other groups (i.e., plesiomorphic characters) to define the Pyralididae. The presence of the ocelli and maxillary palpi are plesiomorphic characters, the proboscis is secondarily lost, the forewing venation is highly variable at lower taxonomic levels (and hence not used by most later workers), and the lack of a hindwing pecten is plesiomorphic.

Ragonot (1891) was the first to separate the Pyralinae and Endotrichinae based on the veins 7 [=Rs] and 8 [=Sc+R<sub>1</sub>] of the hindwing in a key: "Nervures 7 et 8 soudées aux inférieures, très rarement séparées" ["Veins 7 and 8 fused in the hindwings"] keyed to the Chrysauginae and Endotrichiinae and "Nervures 7 et 8 séparées" ["Veins 7 and 8 separate"] keyed to the Pyralidinae (Ragonot 1891:446).

Hampson (1896) included only the Phycitinae, Chrysauginae, Epipaschiinae, Endotrichiinae, and Pyralinae in his concept of the Pyralidae and used some of



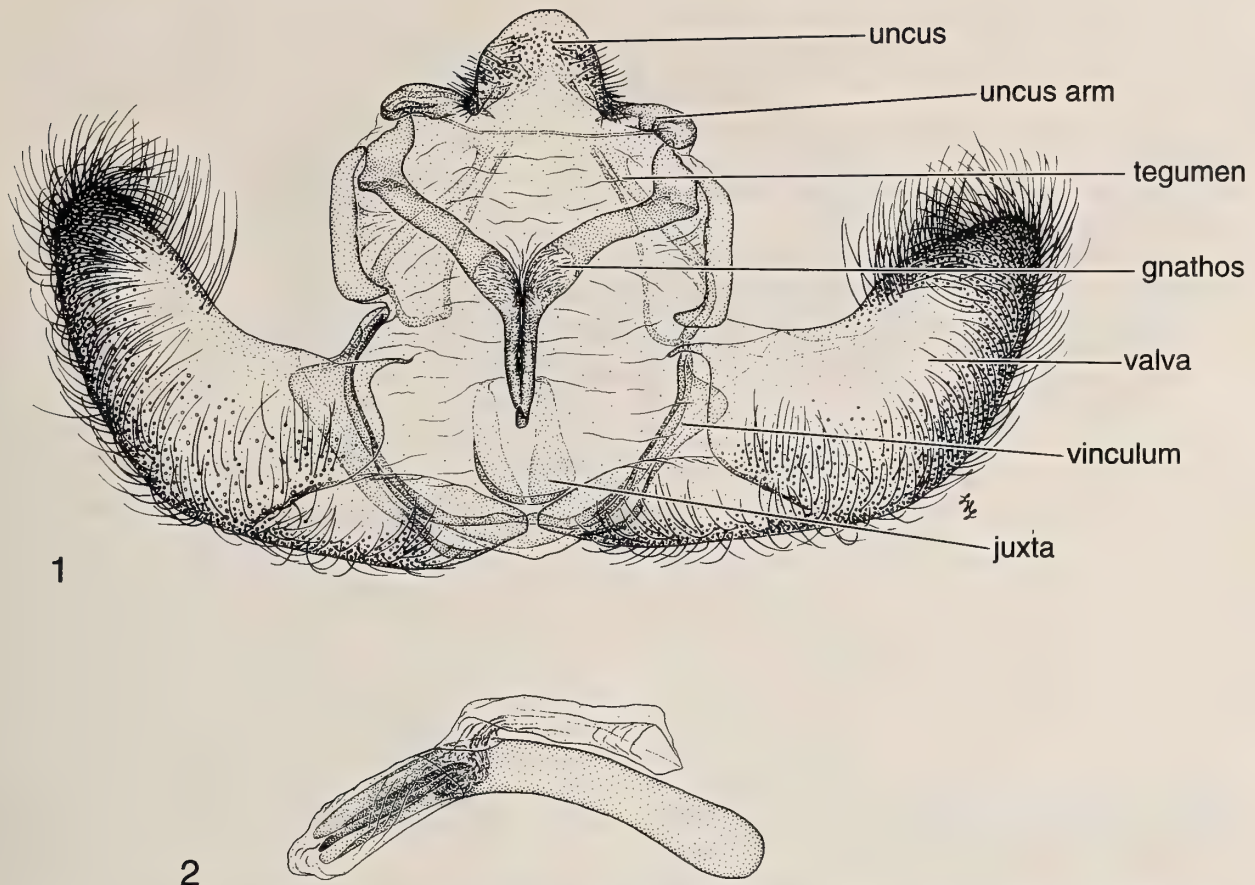


FIG. 1. *Pyralis farinalis* Linnaeus, type species; characteristic male genitalia of Pyralini. FIG. 2. *Pyralis farinalis* Linnaeus, aedeagus.

the same plesiomorphic characters as Meyrick (1890). But he grouped the Epipaschiinae, Endotrichinae and Pyralinae based on the following two characters:

"The three subfamilies of the Pyralidae, the Epipaschiinae, Endotrichinae, and Pyralinae, of which a classification is here attempted, all belong to the group of Pyralidae which have the median nervure of the hindwing non-pectinate on upperside, and vein 7 [=Rs] of the forewing stalked with 8 [=Sc+R<sub>1</sub>]" (Hampson 1896) [italics ours].

The lack of a hindwing pecten is plesiomorphic, and he used the same character (stalked veins 7 [=Rs] and 8 [=Sc+R<sub>1</sub>]) of Ragonot to define the Endotrichinae and Chrysauginae.

The relationship and definition of the endotrichines and pyralines was not addressed again until Whalley (1961), who did not provide characters to define the Pyralinae or the Pyralini. To define the Endotrichini he used the same plesiomorphic characters used by Hampson (1896), with the exception of the presence of the chaetosema, but this state is plesiomorphic as well. The Endotrichinae of Hampson (1896) was described as follows:

"Proboscis well developed; maxillary palpi present; build slender. Forewing with vein 7 stalked with 8, 9 (7 absent in *Hendecasis*).

Hindwing with median nervure non-pectinate; vein 7 [=Rs] anastomosing with 8" [italics ours].

The Endotrichini of Whalley (1961) was described as follows:

"Proboscis well developed, maxillary palps present. Chaetosema present. Forewing with vein R<sub>5</sub> stalked with R<sub>4</sub> and R<sub>3</sub>. Hind wing with median vein non-pectinate. Vein Rs anastomosing with Sc+R" [italics ours].

Munroe and Shaffer (1980) revised three large genera in the Pyralini (Pyralinae). Their definition of the Pyralinae is basically a combination of Hampson's (1896) definition of the Endotrichinae and Pyralinae from a key with Whalley's (1961) rank of tribes. The Pyralinae of Hampson (1896) was described as follows:

"Proboscis usually well-developed; maxillary palpi present and usually filiform. Forewing with vein 7 stalked with 8,9. Hindwing with the median nervure non-pectinate; vein 8 [=Sc+R<sub>1</sub>] free" [italics ours].

The Pyralinae of Munroe and Shaffer (1980) was described as follows:

"The three genera can now be defined as belonging to the Pyralinae from the following characters: chaetosema present; maxillary palpus present; proboscis well developed; fore wing with R5 stalked with R4 and R3; hind wing with Rs not anastomosed with Sc+R<sub>1</sub> (Pyralini), or



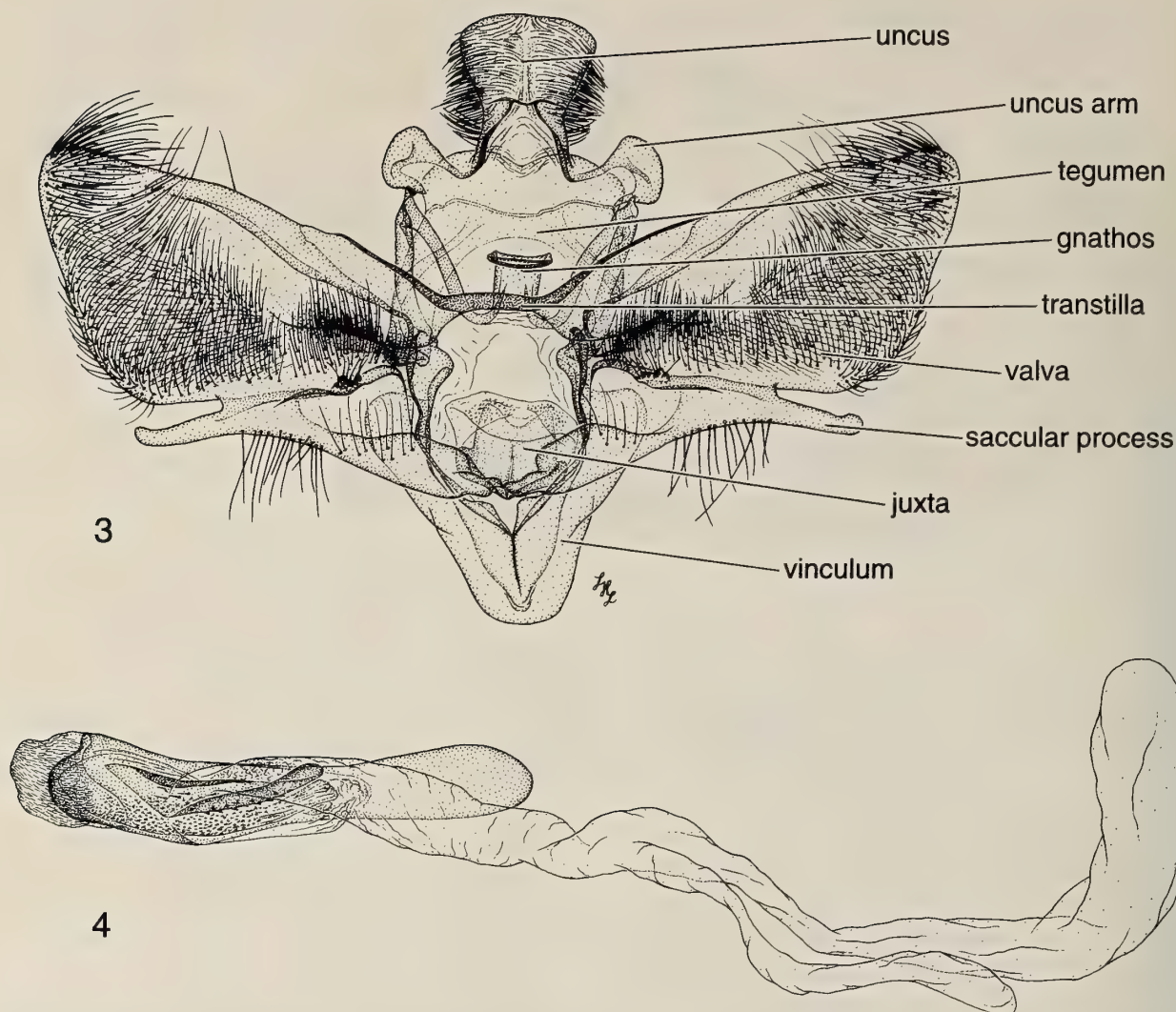


FIG. 3. *Endotricha flammealis* (Denis & Schiffermüller), type species characteristic male genitalia of Endotrichini. FIG. 4. *Endotricha flammealis* (Denis & Schiffermüller), aedeagus.

*Rs* anastomosed with *Sc+R<sub>1</sub>* (*Endotrichini*); median vein non-pectinated" [italics ours].

Whalley (1961) recognized the problem with the definition of the hindwing character that separated the two groups: "In several cases they have been said to anastomose where, as close examination shows, they merely run very close together (e.g., *Rostripalpus* Hampson)." The lack of anastomosis of *Rs* and *Sc+R<sub>1</sub>* varies in other groups within the Pyraloidea besides the Pyralini, and it has been documented as highly homoplasious at the generic level among the genera of the *Pococera* complex of the Epipaschiinae (Solis 1993) and at the species level (Shaffer & Solis 1994). Other groups where the majority of the taxa lack the anastomosis of *Rs* and *Sc+R<sub>1</sub>* but where there are examples where the two veins barely anastomose have

been observed in representatives of the New World Cacotherapiini (Galleriinae) and some genera in the Crambinae (e.g., *Pseudoschoenobius* Fernald). Based on our observations of the distribution of this hindwing character in other groups within the Pyraloidea, distribution of the hindwing character within the Pyralinae, and lack of concurrence with the characters of the male genitalia, we propose that the hindwing venational character is not reliable in the separation or definition of taxa at suprageneric levels in the Pyralinae.

Minet (1982, 1985) was the first to maintain that the Pyralinae were paraphyletic because characters used by past workers were plesiomorphic. He stated: "Les Pyralinae semblent paraphylétiques par rapport à des taxa tels que les Endotrichinae, les Chrysauginae ou les Epipaschiinae (dont ils ne diffèrent que par un en-



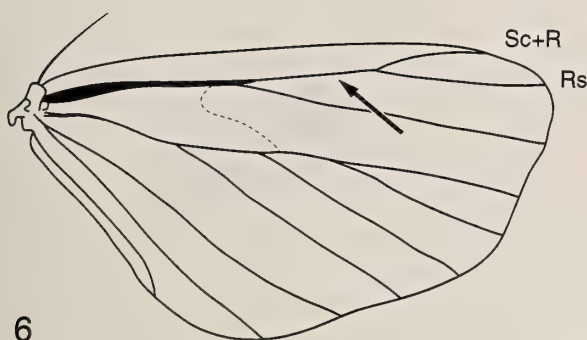


FIG. 5. Wing venation (idealized); arrow indicates lack of anastomosis. FIG. 6. Wing venation (idealized); arrow indicates anastomosis.

semble de caracteres plesiomorphes: palpes maxillaires bien développés, ailes antérieures sans écailles hérissées, etc.),” [“The Pyralinae appear to be paraphyletic in comparison with taxa such as the Endotrichinae, the Chrysauginae or the Epipaschiinae (in that they share a group of plesiomorphic characters: maxillary palpi well developed, forewings without raised scales, etc.)”] but he retained pyralines and endotrichines at the subfamily level. Whalley (1963), in his study of *Endotricha*, found that the retention of Ragonot’s concept of the Endotrichinae as a subfamily was not warranted and proposed the Endotrichinae as a tribe of the Pyralinae. He did not offer a reason or characters to support this conclusion. Solis and Mitter (1992) agreed with Minet that previous characters used to define the two taxa were plesiomorphic states, but they treated the endotrichines as a tribe within the Pyralinae according to Whalley (1961) because Minet (1985), in his study of the tympanal organs, presented no apomorphies for the Pyralinae, Pyralini, or Endotrichini. Solis and Mitter (1992) proposed one character of the female genitalia as a synapomorphy for the Pyralinae, but proposed none for the Pyralini or Endotrichini.

## RESULTS

**Adult genitalic morphology.** Previous authors (Whalley 1961, 1963, Munroe & Shaffer 1980) did not use genitalic characters to define the Pyralinae, Pyralini, or Endotrichini, although they used genitalic morphology at the species level for their studies. Solis and Mitter (1992) proposed a character of the female genitalia (corpus bursae barely extending cephalad beyond segment 7) to support the monophyly of the Pyralinae. This study, however, was based on a small sample size, a character that remains untested.

### Pyralini (Figs. 1, 2, 7):

**Description:** Male: Uncus same width throughout or less narrow than the base, flat or spatulate, ventrally with spine clusters absent; uncus arms laterally not large and earlike; downcurved gnathos with arms strongly developed, with well-developed medial, narrow spike terminating in a small dorsally curved hook; tegumen strongly sclerotized; vinculum well developed; juxta simple, rarely heavily sclerotized, spiny catena (baso-medial portion of anellus) present or absent or laterally sclerotized, and heavily spined, sometimes anellus reflexed with heavy sclerotization; transtilla absent or, if present, membranous, rarely well developed and heavily sclerotized; valva variable in shape, same width to apex or more narrow distally, basal and costal process absent or present, if present well developed or not, without saccular process, ventral surface of valva bearing hairlike setae not arranged in radiating rows, costal setae absent; vesica of aedeagus with or without clusters of spinelike cornuti, vesica sometimes spined, reflexed with heavy sclerotization, or with broad bands of sclerotization its entire length. Female: Segment 8 and associated membranes either short, or long and extensible; apophyses anteriores and posteriores long, stout or slender; ostial end of ductus bursae membranous, with small, well-sclerotized to large, heavily sclerotized compact pouches present or absent; ductus bursae long and narrow with areas of minute spines immediately below antrum or other sclerotized areas; corpus bursae large, signum variable, absent, or if present from scobinate patches, usually within single large area, to long and spinelike.

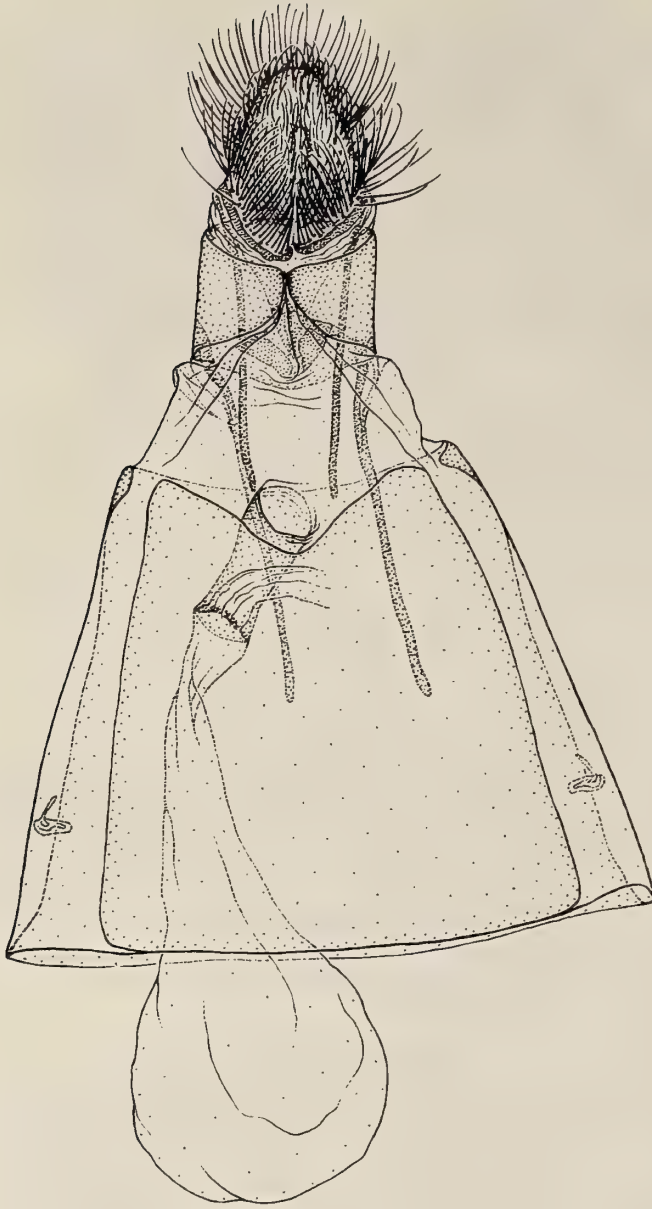
### Endotrichini (Figs. 3, 4, 8):

**Diagnosis:** Uncus broadest at apex; uncus arms laterally large, earlike; gnathos medially broad, spatulate, platelike.

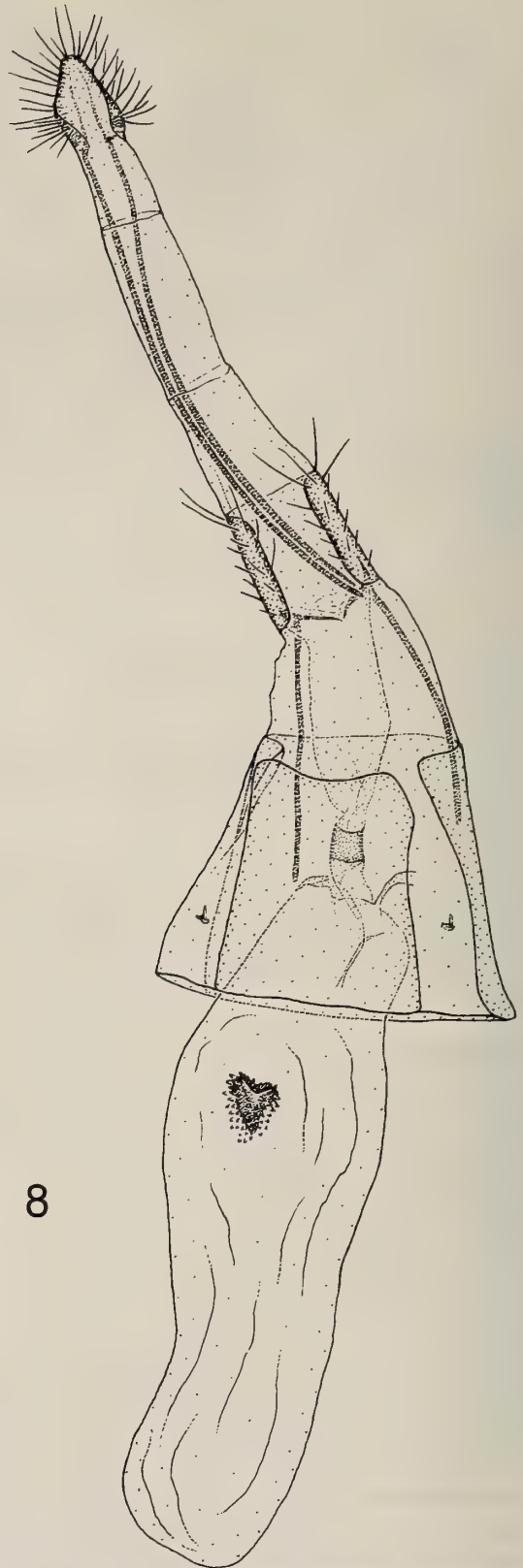
**Description:** Male: Uncus broadest at apex, ventrally with spine clusters present or absent (uncus process of Whalley); uncus arms laterally large, earlike [socii of Whalley; socii, according to Klots (1956) are paired processes on either side of the base of the uncus; these structures are not socii, but the most lateral elements of the uncus arms of the Pyralidae (Solis & Mitter 1992)]; downcurved gnathos arms strongly or weakly developed, usually with a well-developed medial, broad, spatulate, and upturned central plate; weakly sclerotized tegumen; vinculum well developed; juxta simple, sometimes with spiny manica; transtilla present, usually heavily sclerotized; valva usually same width to apex, may bear basal process and saccular process; ventral surface bearing hairlike setae in rows pointing toward base of valva; prominent, reflexed, sometimes spear-shaped costal setae may be present arising from costa near apex; aedeagus with vesica bearing sticklike or clublike cornuti varying in shape and length. Female genitalia: Segment 8 and associated membranes long and extensible; apophyses anteriores and posteriores long and slender; ostial end of ductus bursae minutely spined, without pouches; antrum sclerotized; ductus bursae short, minutely spined, or very long and membranous; corpus bursae large with signum scobinate.

Although we can provide synapomorphies in states of the uncus and gnathos (see diagnosis above) for the Endotrichini in the male





7



8

FIG. 7. *Pyralis farinalis* Linnaeus, type species; characteristic female genitalia of Pyralini. FIG. 8. *Endotricha flammealis* (Denis & Schiffmüller), type species; characteristic female genitalia of Endotrichini.



genitalia, we were unable to find synapomorphies for the Pyralini where the states are either shared with the Endotrichini or with related subfamilies. The genitalic characters of the Pyralinae are either variable at lower taxonomic levels or plesiomorphic, i.e., found in all related subfamilies. We provide a description of the genitalia for Endotrichini and Pyralini because a concept based on the morphology of the male genitalia was used to assign taxa in the Endotrichini and Pyralini in the Australian and Neotropical checklists.

**Larval morphology.** Comparison of the caterpillars of *Endotricha flammealis* with *Pyralis farinalis*, *Aglossa caprealis*, and *Herculia psammioxantha* (with caterpillars of other subfamilies of the Pyralidae as outgroups) did not result in any apomorphic characters to support the monophyly of the Pyralinae, Pyralini, or Endotrichini. Historically, the Hasenfuss (1960) concept of the Pyralinae consisted of present-day galleriines, pyralines, and phycitines (he did not include chrysaugines or epipaschiines in his study); he considered *Endotricha* as a pyraline.

The larvae of *Endotricha* have a pinaculum ring on SD1 of A9, a synapomorphy for the Pyralidae (the plesiomorphic state, the absence of the pinaculum ring on SD1 of A9, occurs in the Crambidae). In sum, we found that *E. flammealis* larvae lack the unique characters assigned to other subfamilies and have the same plesiomorphic setal character states assigned to the larvae of the Pyralinae. The Epipaschiinae and Pyralinae both lack a pinaculum ring on any other segment other than A9 (in comparison to the presence of a pinaculum ring on T2 of the Phycitinae, T3 of the Chrysauginae, and A1 of the Galleriinae; presence in each segment is the derived state, although the pinaculum has been secondarily lost in several genera and/or species of each subfamily). Based on work by Hasenfuss (1960) and Allyson (1977) the Epipaschiinae and Pyralinae are separated from each other by the distance between the ventral setae on A7 and A9. In the Epipaschiinae the two ventral setae are closer together on A7 than those on A9 and in the Pyralinae the two ventral setae on A7 and A9 are equidistant (the plesiomorphic condition shared by other subfamilies of the Pyralidae).

**Taxonomic placement of genera.** Recently, genera from southeast Asia and Australia previously placed in the Endotrichinae with anastomosed Rs and Sc+R<sub>1</sub> in the hindwing, but with genitalic characteristics of the Pyralini were transferred to the Pyralini in the Australian checklist (Shaffer et al. 1996) based on the genitalia morphology. Those genera transferred from the Endotrichinae to the Pyralinae were based on the genitalia morphology: *Gauna* Walker, *Curena* Walker, *Arescoptera* Walker, *Scenedra* Meyrick, *Tanyethira* Turner, *Scenidiopsis* Turner, *Perisseretma* Warren, and *Perula* Mabilie.

According to the definition based on genitalic morphology given above, there are no known species of Endotrichini in the Western Hemisphere, but four genera, *Perforadix* Sein, *Micronix* Amsel, *Micromastra* Schaus, and *Taboga* Dyar have been historically placed within the Endotrichinae due to the anastomosing of Rs and Sc+R<sub>1</sub> in the hindwing. *Perforadix*, *Micronix*, and *Micromastra* were inadvertently excluded from the Neotropical Pyraloidea checklist (Shaffer & Solis 1995). *Taboga* was included in the Neotropical checklist, but needed to have its position in the Pyralinae verified. We found that *Perforadix* belongs in the Pyraustinae and *Micronix* belongs in the Crambinae, both hereby transferred, and, of the four, only *Micro-*

*mastra* and *Taboga* remain in the Pyralinae. Table 2 is a complete list of the Pyralinae (Pyralini) of the Western Hemisphere (Munroe 1983, Shaffer & Solis 1995).

Sein (1930) placed *Perforadix sacchari* Sein, commonly known as the Sugarcane root caterpillar, in the Endotrichinae. This species is a major pest of sugar cane in Puerto Rico and nearby islands. Sein (1930) illustrated the morphology of all life stages in great detail and described its biology and methods of control. The author failed to designate types or even list type specimens, but we found seven specimens each with a small label "P.R./Sein" and a red label "Cotype/Cornell U. No. 6087" at Cornell University. According to Sein (1930), W. T. M. Forbes, who was at Cornell University at the time, identified the material and presumably he also labelled the material as cotypes. We designate one specimen (male) as the lectotype and the other 6 specimens as paralectotypes (material in poor condition, abdomens are missing), and they are labelled as such in the collection at Cornell University. We studied additional material collected by Sein, identified by H. G. Dyar, as stated by Sein (1930), and dissections by Carl Heinrich at the USNM and found that *Perforadix* is a synonym of *Sufetula* Walker, **new synonymy**, in the Pyraustinae. We discovered that based on the morphology of the tympanal organs (i.e., crambid "open" tympanal organs with a praecinctorium) it belongs in the Crambidae. Based on the external and genitalic morphology after comparison with other species in the genus, including the type species, it belongs in the genus *Sufetula* Walker. It is interesting to note that *P. sacchari* was originally identified for Sein by H. G. Dyar as *Sufetula grumalis* Schaus, a species presently placed in *Sufetula* (Munroe, 1995:76). We also examined another species, *Sufetula pygmaea* Hampson, and found it does not belong in the Pyraloidea, but in the Noctuidae (Nolinae): *Nola pygmaea* (Hampson), **new combination**.

Amsel (1956) described *Micronix nivalis* in the Endotrichinae. Nothing is known about the biology of this Venezuelan species. We were unable to locate the type, a male, but Amsel provided a photograph of the adult and poor line drawings of the male genitalia and wings. The hooded uncus and the costal process of the male genitalia characteristic of crambines are very evident in the illustration; therefore, we transfer this monotypic genus to the Crambinae. Although we cannot determine its placement within the Crambinae, we suggest that it belongs in the tribe Crambini.

Schaus (1940) placed *Micromastra isoldalis* in the Endotrichinae. Nothing is known about the biology of this Puerto Rican species. Dyar (1914) described *Taboga inis* in the Endotrichinae. The type series is from



TABLE 2. Pyralini (Pyrilidae: Pyralinae) of the Western Hemisphere

<b>Aglossa</b> Latreille, [1796]	
<i>Euchita</i> Hübner, [1825]	
<i>Agriope</i> Ragonot, 1894	
<i>acallalis</i> Dyar, 1908	
<i>baba</i> Dyar, 1914	
<i>cacamica</i> (Dyar, 1913) ( <i>Pyralis</i> )	
<i>caprealis</i> (Hübner, [1800–09]) ( <i>Pyralis</i> )	
<i>capreolatus</i> Haworth, 1809	
<i>cuprealis</i> Hübner, [1825], missp.	
<i>aenalis</i> (Costa, 1836) ( <i>Pyralis</i> )	
<i>domalis</i> Guenée, 1854	
<i>incultella</i> (Walker, [1866]) ( <i>Acrobasis</i> )	
<i>enthealis</i> (Hulst, 1886) ( <i>Tetralopha</i> )	
<i>cuprialis</i> Heinrich, 1931, missp.	
<i>costiferalis</i> (Walker, 1886) ( <i>Pyralis</i> )	
<i>costigeralis</i> (Walker, [1865]) ( <i>Pyralis</i> ), preocc. (Walker, 1862)	
<i>cuprina</i> (Zeller, 1872) ( <i>Pyralis</i> )	
<i>disciferalis</i> (Dyar, 1908) ( <i>Pyralis</i> )	
<i>electalis</i> Hulst, 1866	
<i>furva</i> Heinrich, 1931	
<i>gigantalis</i> Barnes & Benjamin, 1925	
<i>oculalis</i> Hampson, 1906	
<i>pinguinialis</i> (Linnaeus, 1758) ( <i>Pyralis</i> )	
<i>marmorella</i> (Geoffroy, 1785) ( <i>Tinea</i> )	
<i>marmoratella</i> (Villers, 1789) ( <i>Tinea</i> )	
<i>pinguiculatus</i> (Haworth, 1809) ( <i>Crambus</i> )	
<i>guicciardii</i> Constantino, 1922	
<b>Arispe</b> Ragonot, 1891	
<i>Uscodys</i> Dyar, 1909	
<i>cestialis</i> (Hulst, 1886) ( <i>Anerastia</i> )	
<i>atalis</i> (Dyar, 1908) ( <i>Uscodys</i> )	
<i>concretalis</i> Ragonot, 1891	
<i>ovalis</i> Ragonot, 1891	
<b>Catocrocis</b> Ragonot, 1891	
<i>Catocrocis</i> Ragonot, 1892, missp.	
<i>lithosialis</i> Ragonot, 1891	
<b>Dolichomia</b> Ragonot, 1891	
<i>amoenalis</i> (Möschler, 1882) ( <i>Asopia</i> )	
<i>isidora</i> (Meyrick, 1936) ( <i>Pyralis</i> )	
<i>binodulalis</i> (Zeller, 1872) ( <i>Asopia</i> )	
<i>craspedalis</i> (Hampson, 1906) ( <i>Tegulifera</i> )	
<i>datames</i> (Druce, 1900) ( <i>Pyralis</i> )	
<i>decectalis</i> (Druce, 1900) ( <i>Pyralis</i> )	
<i>grafialis</i> (Snellen, 1875) ( <i>Asopia</i> )	
<i>impurpuratalis</i> (Dognin, 1910) ( <i>Pyralis</i> )	
<i>nigrapuncta</i> (Kaye, 1901) ( <i>Pyralis</i> )	
<i>olinalis</i> (Guenée, 1854) ( <i>Pyralis</i> )	
<i>trentonalis</i> (Lederer, 1863) ( <i>Asopia</i> )	
<i>himonialis</i> (Zeller, 1872) ( <i>Asopia</i> )	
<i>infimbrialis</i> (Dyar, 1908) ( <i>Herculia</i> )	
<i>phanerostola</i> (Hampson, 1917) ( <i>Paractenia</i> )	
<i>planalis</i> (Grote, 1880) ( <i>Asopia</i> )	
<i>enniculis</i> (Hulst, 1886) ( <i>Asopia</i> )	
<i>occidentalis</i> (Hulst, 1886) ( <i>Asopia</i> )	
<i>plumbeoprunalis</i> (Hampson, 1917) ( <i>Herculia</i> )	
<i>resectalis</i> (Lederer, 1863) ( <i>Asopia</i> )	
<i>thymetusalis</i> (Walker, 1859) ( <i>Botys</i> ) <b>New combination</b>	
<i>devialis</i> (Grote, 1875) ( <i>Asopia</i> )	
<i>vernaculalis</i> (Berg, 1874) ( <i>Asopia</i> )	
<b>Herculia</b> Walker, 1859	
<i>Buzala</i> Walker, 1863	
<i>Cisse</i> Walker, 1863	
<i>Bejuda</i> Walker, [1866]	
<i>Bleone</i> Ragonot, 1890	
<i>Herculea</i> Amsel, 1956 [index], missp.	
<i>tabidalis</i> (Warren, 1891) ( <i>Pyralis</i> )	
<b>Hypsopygia</b> Hübner, [1825]	
<i>costalis</i> (Fabricius, 1775) ( <i>Phalaena</i> )	
<i>fimbrialis</i> ([Denis & Schiffermüller], 1775) ( <i>Pyralis</i> )	
<i>purpurana</i> (Thunberg, 1784) ( <i>Tortrix</i> )	
<i>hyllalis</i> (Walker, 1859) ( <i>Pyralis</i> )	
<b>Mapeta</b> Walker, 1863	
<i>Homalochroa</i> Lederer, 1863	
<i>cynosura</i> Druce, 1895	
<i>omphephora</i> Dyar, 1914	
<i>schausi</i> Druce, 1895	
<i>xanthomelas</i> Walker, 1863	
<i>aestivalis</i> (Lederer, 1863) ( <i>Homalochroa</i> )	
<i>divisa</i> (Boisduval, 1870) ( <i>Pyrilopsis</i> )	
<b>Micromastra</b> Schaus, 1940	
<i>isoldalis</i> Schaus, 1940	
<b>Neodavisia</b> Barnes & McDunnough, 1914	
<i>Davisia</i> Barnes & McDunnough, 1913, preocc. (Del guercio, 1909 [Hemiptera])	
<i>melusina</i> Ferguson, Blanchard, & Knudson, 1984	
<i>singularis</i> (Barnes & McDunnough, 1913) ( <i>Davisia</i> )	
<b>Ocrasa</b> Walker, [1866]	
<i>Parasopia</i> Möschler, 1890	
<i>nostralis</i> (Guenée, 1854) ( <i>Pyralis</i> )	
<i>helenensis</i> (Wollaston, 1879) ( <i>Pyralis</i> )	
<i>tenuis</i> (Butler, 1880) ( <i>Pyralis</i> )	
<i>dissimilalis</i> (Möschler, 1890) ( <i>Parasopia</i> )	
<i>sordidalis</i> (Barnes & McDunnough, 1913) ( <i>Herculia</i> )	
<i>psammioxantha</i> (Dyar, 1917) ( <i>Herculia</i> )	
<i>venezuelensis</i> (Amsel, 1956) ( <i>Herculia</i> )	
<i>tripartitalis</i> (Herrich-Schäffer, 1871) ( <i>Asopia</i> )	
<b>Pseudasopia</b> Grote, 1873	
<i>cohortalis</i> (Grote, 1878) ( <i>Asopia</i> )	
<i>florencealis</i> (Blackmore, 1920) ( <i>Herculia</i> )	
<i>intermedialis</i> (Walker, 1862) ( <i>Pyralis</i> )	
<i>sodalis</i> (Walker, 1869) ( <i>Pyralis</i> )	
<i>squamealis</i> Grote, 1873	
<i>phoezalis</i> (Dyar, 1908) ( <i>Herculia</i> )	
<b>Pyralis</b> Linnaeus, 1758	
<i>Aletes</i> Rafinesque, 1815, nom. nud.	
<i>Ceropsina</i> Rafinesque, 1815, nom. nud.	
<i>Spyrella</i> Rafinesque, 1815, repl. name	
<i>Asopia</i> Treitschke, 1828	
<i>Sacatia</i> Walker, 1863	
<i>Eutrichodes</i> Warren, 1891	
<i>farinalis</i> Linnaeus, 1758	
<i>domesticalis</i> (Zeller, 1847) ( <i>Asopia</i> )	
<i>fraterna</i> Butler, 1879	
<i>manihotalis</i> .- Matsumura, 1900 (not Guenée, 1854)	
<i>meridionalis</i> Schmidt, 1934	
<i>orientalis</i> Amsel, 1961	
<i>manihotalis</i> Guenée, 1854	
<i>vetusalis</i> Walker, [1859]	
<i>gerontesalis</i> Walker, [1859]	
<i>laudatella</i> (Walker, 1863) ( <i>Sacatia</i> )	
<i>despectalis</i> Walker, [1866]	
<i>miseralis</i> Walker, [1866]	
<i>achatina</i> Butler, 1877	
<i>haematinalis</i> (Saalmüller, 1880) ( <i>Asopia</i> )	
<i>gerontialis</i> (Meyrick, 1888) ( <i>Asopia</i> ), emend.	
<i>centripunctalis</i> (Gaede, 1916) ( <i>Endotricha</i> )	
<i>pupalis</i> Strand, 1919	
<i>compsobathra</i> Meyrick, 1932	
<b>Taboga</b> Dyar, 1914	
<i>inis</i> Dyar, 1914	



Panama. Study of the genitalia of the type series at the USNM of both of these species confirm their placement within the Pyralini, and not in the Endotrichini.

In the Australian checklist (Shaffer et al. 1996:173) the headings of the Endotrichini and Pyralini were mislabeled and difficult to change at proof stage. The Endotrichinae should have been titled the Endotrichini and placed under the heading of the Pyralinae. In addition, the genus *Macna* Walker was inadvertently included in the Pyralinae (Pyralini), but it should have been placed in the Chrysauginae. In the Neotropical checklist (Shaffer & Solis 1995:80) the Pyralini should have been included as a subheading under Pyralinae to indicate the tribal placement of the genera found in the Western Hemisphere.

#### DISCUSSION

The Pyraloidea, one of the larger superfamilies of the Lepidoptera, has over 15,000 described species, yet much remains to be done in taxonomy, and, more so, with the phylogenetic relationships. A taxonomic study usually begins with a checklist or a catalogue of described species as an inventory to document those that have already been described. A checklist may refine the placement of taxa and can clearly mark taxon transfers, as well as provide other information, such as misplaced taxa. By definition, a checklist or catalog does not adequately state or discuss the taxonomic problems solved or those that remain to be solved.

We have described the morphological reasons for the placement of taxa in the Pyralini or Endotrichini in two checklists (Shaffer et al. 1996, Shaffer & Solis 1995). We have also summarized the taxonomic and phylogenetic status of the two tribes included in the Pyralinae. The genitalia of the Endotrichini are clearly different from those of the Pyralini, but authors have dealt only with a few genera in both taxa and, as we have shown, have used the same plesiomorphic or homoplasious characters since Meyrick (1890) to define higher level taxa. We retain the two tribes in the classification system for the sake of stability and retention of character information, but acknowledge that the Pyralini is likely a paraphyletic group. Moreover, a preliminary study of an independent character set, the larval stage, provides no obvious synapomorphies for the Pyralinae or the Pyralini.

Our observations of the genitalia and larvae of the Pyralini and Endotrichini are made with the expectation that they may prove useful in a future phylogenetic study of the Pyralini genera that includes an entire suite of adult and immature characters. Any future study should also include pupal and perhaps behav-

ioral characters, although caution is suggested concerning the latter due to the convergent nature of behavioral characters. A phylogenetic analysis of the genera of the Pyralini would be the first attempt to test the paraphyly of the Pyralini with respect to the Endotrichini, with the possibility that results may also invalidate the traditional tribal concept. Such a study may also provide characters to support the monophyly of the Pyralinae.

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## POPULATION BIOLOGY AND WING COLOR VARIATION IN *HELICONIUS ERATO PHYLLIS* (NYMPHALIDAE)

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**ABSTRACT.** Twenty-six months of mark-recapture study of three populations of *Heliconius erato phyllis* in SE Brazil showed these populations to be relatively stable through time. The adults showed high longevity, similar to that of other tropical *Heliconius*. Sex ratio was male biased, and males showed longer residence times than females. The number of red raylets on the ventral hindwing showed seasonal variation, considered to be numeric polyphenism. Of all the species of *Heliconius*, *H. erato* is proposed to be the most tolerant of variation in habitat, larval and adult resources ("ecological plasticity"). These traits are proposed as reasons for the wide distribution of this species in tropical America.

**Additional key words:** mark-recapture, Heliconiini, Passifloraceae, red raylets, polyphenism.

Even if Heliconiine butterflies are among the best-studied tropical insects, with much known about their systematics, population ecology, behavior, immature biology, host plant relationships, coevolution, mimicry, chemistry, genetics, and conservation (Ehrlich and Gilbert 1973, Brown & Benson 1974, Gilbert 1975, Araujo 1980, Brown 1981, Turner 1981, Sheppard et al. 1985, Mallet 1986a, 1986b), data are not available for most species and geographic populations of *Heliconius*; and generalizations based on other well-known species and regions may fail to explain local patterns and processes. For example, the current idea that *Heliconius* maintain relatively stable population numbers through time (based mainly on Turner 1971 and Ehrlich & Gilbert 1973) is not true for *Heliconius erato phyllis* (F.) near the limits of its range in temperate southern Brazil (Saalfeld & Araujo 1981).

*Heliconius erato* is the most widespread species of the genus, present in several different habitats and forest types from Mexico to north Argentina (Emsley 1964, 1965), and its subspecies *phyllis* has the widest geographic distribution (Brown 1979, Sheppard et al. 1985) and environmental tolerances (Araujo 1980). In the southern populations of *H. erato* (30°S), periodic variation in several features of wing color pattern, especially the hindwing red-raylets, has also been noted (Pansera & Araujo 1983, Oliveira & Araujo 1992). The present study describes features of a population of *H. erato phyllis* in a subtropical rainforest in southeastern Brazil (24°S), 6° (660 km) farther north of the southern limits of the species distribution, and reports cyclical annual variation in two wing color-pattern elements.

### STUDY SITES AND METHODS

A mark-release-recapture (MRR) study was carried out in three areas in São Paulo state, southeastern Brazil. The main study area was "Morro do Voturuá" (MV) (46°22'W, 23°57'S), in the city of São Vicente (Fig. 1). The site was originally covered with lowland subtropical rainforest (Ururahy et al. 1987). The annual rainfall reaches 2500 mm and the average annual temperature is 21°C (Setzer 1949, Prodesan 1969, Nimer 1972), with the mean of the coldest month 18.2°C and of the warmest month 25.3°C (Santos 1965) (Fig. 2, methods following Santos 1965 and Walter 1985). Most of the area is covered by secondary forest on low hills (100–200 m elevation). Similar work was done in two nearby sites: the "Vale do Rio Quilombo" (VQ, Fig. 1), a road along a river valley with much secondary vegetation and flowers, 12 field days over three months; and the "Morro do Japu" (MJ, Fig. 1), a large hill facing the ocean SW of MV with similar vegetation, 47 field days over seven months (see details on these areas in Freitas 1993).

Mark-release-recapture studies were made in Morro do Voturuá during 26 months, from 13 August 1994 to 30 September 1996, 1–4 times per week, totaling 153 field days (about 4 hours/day). Butterflies were captured with an insect net, individually numbered on the underside of both forewings (in the red central macula) with a black permanent felt-tipped pen, and released. Age (based on wing wear), forewing length (in mm), point of capture, sex and food sources were recorded (as in Freitas 1993, 1996). The age of individual butterflies was estimated based on wing wear, initially using the six categories described by

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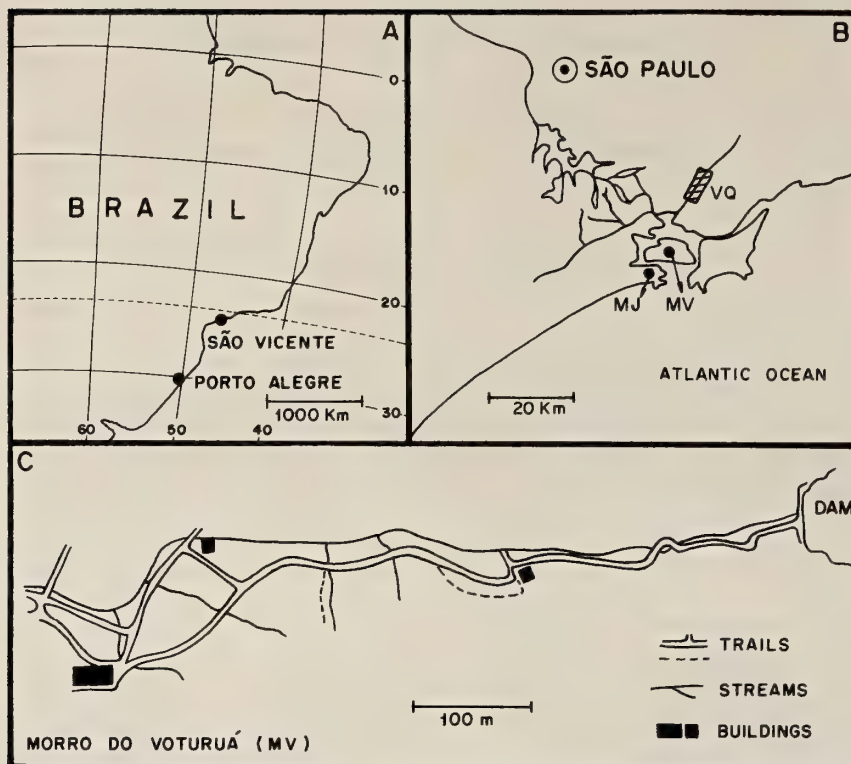


FIG. 1. (A) study area (São Vicente Region) in Southeastern Brazil. In regional map (B), VQ = Vale do Rio Quilombo, MJ = Morro do Japuí, MV = Morro do Voturuá (details in C).

Ehrlich and co-workers (Ehrlich & Davidson 1960, Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973). These six categories (freshly emerged, new, intermediate, old, very old, tattered) were regrouped into three categories: new = freshly emerged and new individuals, intermediate = intermediate individuals, and old = old, very old, tattered (as in Freitas 1993, 1996). Age structure was calculated as the daily proportion of each category, and grouped into monthly means. Three wing-color-pattern elements were recorded (Fig. 3): the number of red basal spots, the number and shape of the red raylets on the ventral hindwing, and the color and size of the spot in the inner angle of space Cu1–Cu2 (“cubital spot”) on the dorsal forewing (nomenclature following Miller 1970). Data from August and September 1994 at MV were regarded as the “Winter 1994” sample; each of the following seasons represents observations for 3 consecutive months.

The MRR data from MV were analyzed by the Jolly-Seber method (Southwood 1971) for estimating population parameters (software developed by R. B. Francini, UNISANTOS). In most cases, only males were analyzed because of the low number of females. Daily results were tabulated as “number of individuals captured per day” (NICD), and “number of individu-

als present per day” (NIPD). To estimate the NIPD, recaptured individuals were considered to be present in the population on all previous days since the day of first capture (=marked animals at risk).

## RESULTS

### Population Dynamics

In Morro do Voturuá, the NICD for males varied from one to 13 (mean = 5.9, SD = 2.4;  $n = 153$  days), with 19 days with  $n = 3$  and 13 days with  $n = 10$  males (Fig. 4). The number of newly marked individuals captured in each month (=monthly recruitment) also varied, more in the first year than in the second (Fig. 5). In nearby Morro do Japuí, the male NICD ranged from 1 to 5 (mean = 2.3, SD = 1.1,  $n = 47$  days). The area covered in these two sites is similar (Fig. 1, see also Freitas 1993).

In Vale do Rio Quilombo, the NICD for males was greater than in Morro do Voturuá (mean = 14.5, SD = 4.1,  $n = 12$  days) (Fig. 6A). The area covered in this site was about six times greater than in the previous two, corresponding closely to the NICD ratio for Morro do Japuí (6.3) and suggesting an equivalent density, 40% of that in Morro do Voturuá.

Jolly-Seber analysis for males in Morro do Voturuá (Fig. 7) gave estimated numbers from 3 to 88 individ-



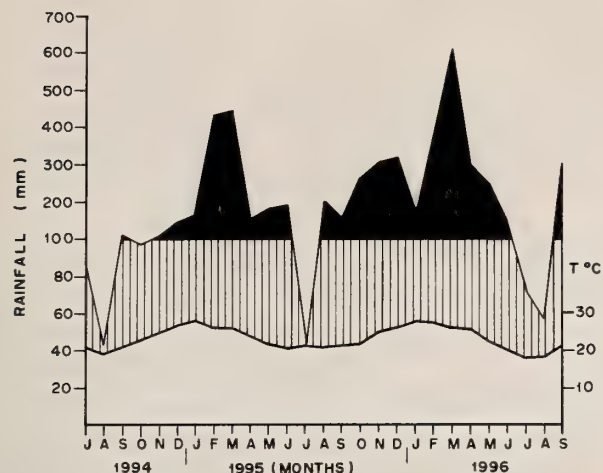


FIG. 2. Climatic diagram of the São Vicente Region during the study period (format following Santos 1965 and Walter 1985). Hatched = humid periods, black = superhumid periods.

uals (mean = 13.5, SD = 9.9,  $n = 152$ ), with most days ( $n = 90$ ) between 10 and 30. The NIPD for males in the same site ranged from 1 to 20 (mean = 9.8, SD = 3.8,  $n = 154$ ). The male population was stable throughout the year, with small fluctuations in number of individuals apparently not related to season, but with lower numbers of individuals observed at the end of winter in the three years (Figs. 4, 5).

The results show that NIPD is better than NICD as an index of population size. In species with stable populations composed of long-lived resident individuals, efficient marking and recapture can give nearly equal population size estimates by the Jolly-Seber method and simple NIPD.

#### Sex Ratio

The sex ratio of individuals captured and marked was male biased in all sites (Table 1, Figs. 6B and 8). In MV males dominated in all but one month of the study; all the captured individuals were male in four months, including April of both years (Fig. 8). In all, 263 males and 74 females were captured and marked. Males were recaptured from one to 16 times and females from one to five times; 154 males and 30 females were recaptured at least once. The proportion of recaptured males (58.5%) was statistically the same as that of females (40.1%) ( $\chi^2 = 2.6$ ,  $df = 1$ ,  $P > 0.20$ ). In VQ the proportions of recaptures of males (30.8%) and females (30.5%) were equal.

#### Age Structure

Comparing the new individuals vs. intermediate+old, most of the first captures in MV were of "new" individuals from both males (71%), and females (54%)

new), even if this number was considered greater in males ( $\chi^2 = 7.6$ ,  $df = 1$ ,  $P < 0.005$ ). Most of the butterflies captured on each day (after the first) were previously marked individuals (mean = 71.4%, SD = 23.4,  $n = 152$  days). The age structure during the 26 months in MV was not stable, with decreases in proportion of "new" individuals in the winter (Fig. 9).

In VQ, the proportion of recaptures/day was high (Fig. 6C), and the age structure quite stable (Fig. 6D), but these results should be taken with care due to the short period of study.

#### Residence Time

In MV, males had a longer residence time (mean = 37.6 days, SD = 25.8,  $n = 154$ ) than females (mean = 22.6 days, SD = 23.0,  $n = 30$ ) ( $t = 2.96$ ,  $df = 182$ ,  $p = 0.004$ ). Estimated residence time of males ("life expectancy" of Cook et al. 1967) was 28.1 days. The maximum individual permanence (survival) was at least 127 days for a male and 89 days for a female (Table 2). In MJ, residence time was calculated only for males (mean = 18 days, SD = 14.6,  $n = 22$ ), since the recapture rate of females was low (only 3 recaptures). In VQ maximum permanence could not be calculated (due to the short period of study and low number of recaptures), but the residence time for males (mean = 20.1 days, SD = 12.8,  $n = 32$ ) and females (mean = 15.0 days, SD = 10.6,  $n = 11$ ) were not significantly different ( $t = 1.17$ ,  $df = 41$ ,  $p = 0.248$ ).

#### Vagility

In MV, most adults showed home range behavior, being observed in the same site for several days, often using the same flower resources. The total distance

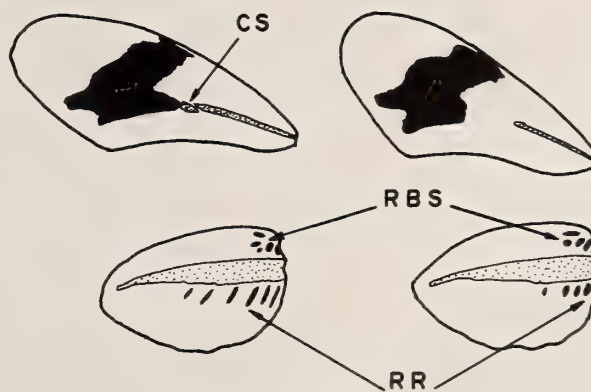


FIG. 3. Wing pattern variation in *Heliconius erato phyllis* (background black, solid = red, dotted = yellow). Colored spot in the inner angle of space Cu1-Cu2 (cubital spot, CS) present (left, red macula almost fused with this), or absent (right). Five basal red spots (RBS) and six red raylets (RR) shaped like small lines (left); four basal red spots and four red raylets shaped like dots (right).



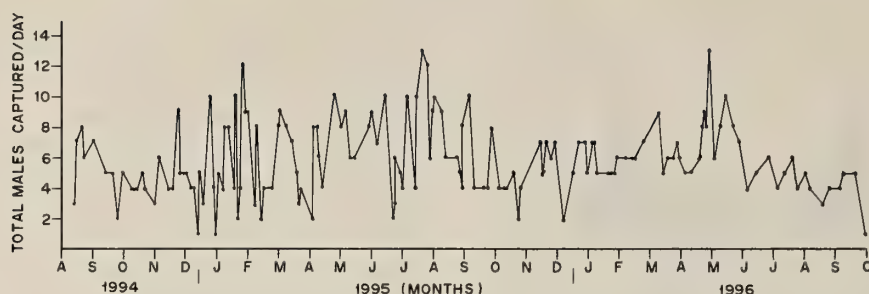


FIG. 4. Daily captures for males of *H. erato phyllis* in Morro do Voturuá, August 1994 to September 1996.

flown by adults varied among individuals. In general, two classes of individuals could be identified: those always observed in the same site (residents) and those seen in two or more separate points in the study area (vagile). Most of the males (71%) and females (85%) recaptured were vagile, while among the residents, some individuals appeared to have tightly restricted home ranges. One male was captured 17 times (twice on the same day) at the same place, and at least half of the resident individuals were captured more than 4 times. The distance traveled by vagile individuals varied from 50 to 660 m (mean = 270.6, SD = 122.9 m,  $n = 97$ ) for males, and 80 to 600 m (mean = 236.3, SD = 140.9,  $n = 23$ ) for females (Table 3). Some individuals showed great mobility in a single day. In one case, one male captured at 0900 was observed 500 m away at 1000 h, returning at 1030 h to within 50 m of the first site of capture. Males were commonly seen near nectar sources and females were mostly observed near the larval food plants.

#### Wing Size and Color Pattern in Morro do Voturuá

Four or five red basal spots are present on the ventral hindwing of *Heliconius erato* butterflies. This trait was very stable, as only three out of 337 individuals analyzed (males and females) showed the fifth basal spot (Fig. 3).

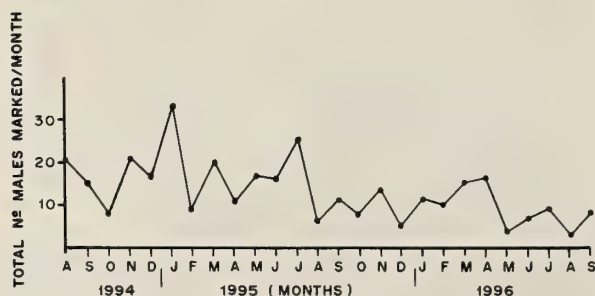


FIG. 5. Monthly recruitment of males of *H. erato phyllis* in Morro do Voturuá, August 1994 to September 1996, as total number of individuals marked for the first time in each month.

The number of red raylets in butterflies of both sexes showed a bimodal distribution, ranging from one to seven, with peaks at three and five (Table 4). The average number increases in summer and autumn and decreases in winter and spring (Table 4).

The shape of the red raylets varied from a rounded dot to a small red line. Individuals with red raylets shaped like dots (65.8%) were more frequent than those with lines (34.2%). The proportions of each type also varied throughout the year (Fig. 10A).

The cubital spot on the dorsal forewing could be absent, present, or fused with the transverse subapical red bar. If present and not fused, the spot could be red or yellow. This character was very variable, but there was a clear majority of "spot to be present and yellow", with no regular pattern of variation throughout the year (Fig. 10B).

The forewing length of males ranged from 27 to 42 mm, the average varying along the year, with greatest values being observed during the summer (Fig. 11).

The average forewing length of males (mean = 36.25 mm, SD = 2.99,  $n = 250$ ) was greater than that of females (mean = 35.21 mm, SD = 2.96,  $n = 71$ ;  $t = 2.58$ ,  $df = 319$ ,  $p = 0.01$ ). This difference was not found when only recaptured individuals were considered ( $t = 1.31$ ,  $df = 181$ ,  $p = 0.191$ ). When comparing the recaptured vs. not recaptured within sexes, recaptured individuals were smaller. This difference was almost significant for males ( $t = 1.933$ ,  $df = 248$ ,  $p = 0.054$ ), but not for females ( $t = -0.172$ ,  $df = 2.83$ ,  $p = 0.864$ ).

#### Natural History of Adults

Adults began activity around 0800 h in summer and 0930 h in winter, but this could vary within a season according to the weather. On some cold days during winter, activity began only after 1030 h.

Beak marks (from handling and release by, or escape from, bird predators) were found on the wings of individuals from all populations, but a different proportion of individuals with damaged wings was ob-



TABLE 1. Sex ratio of marked individuals of *H. erato phyllis* in the three study sites.

Study site	Males	Females	Sex ratio	$\chi^2$ values
Morro do Voturuá	263	74	3.5:1	105.9
Morro do Japuí	50	6	8.3:1	34.6
Vale do Rio Quilombo	104	36	3:1	33

served in each site. Beak marks were seen in MV on 18 males (6.8%; 14 later recaptured) and 1 female (1.3%); in MJ, on 10 males (20%) and no females; in VQ, on 18 males (17%) and 8 females (22%).

Adults were almost always observed feeding on flowers, but a few individuals were observed feeding on damaged fruits of *Rubus rosaefolius* Smith (Rosaceae), and in one case a captured individual was observed bearing a seed of this plant on its proboscis. The most visited flower in the MV site was *Lantana camara* L. (Verbenaceae) (more than 150 records). Two varieties of *L. camara* occur in the study area, one with red-yellow flowers and the other (much more common) with white flowers. Some individuals were also observed visiting flowers of *Rubus rosaefolius* (30 records), *Asclepias curassavica* L. (Asclepiadaceae) (13 records), *Epidendrum fulgens* Brongn. (Orchidaceae) (3 records), *Gurania* sp. (Cucurbitaceae) (3 records), and *Impatiens walleriana* Hook. f. (Balsaminaceae) (2 records). Pollinia of *Epidendrum fulgens* and *Asclepias curassavica* were observed attached to the proboscis of some captured individuals. A new male was once observed visiting the inflorescence of *Heliconia* sp. (Musaceae). Individuals in MV were rarely observed feeding on flowers of Asteraceae, although several species of *Mikania*, *Eupatorium*, and *Vernonia* are common there. The few Asteraceae that were observed being visited include *Mikania lundiana* D.C. (3 records), *Trixis antimenorrhoea* Mart. ex. Baker (3 records), *Eupatorium laevigatum* D.C. (3 records), and *Emilia sonchifolia* D.C. (2 records). In the VQ site (where *L. camara* is not so common), the Asteraceae *Bidens pilosa* L. and *Tithonia speciosa* Hook. ex Gris. were the most visited species with 90 and 45 feeding records respectively. Also in this site *Stachytarpheta polyura* (L.) (Verbenaceae) was commonly used (15 records). Some adults in MV appeared to show "trap-line" (learned sequence) behavior for gathering pollen and nectar (see Ehrlich & Gilbert 1973 and Ehrlich 1984).

Over a two-month period, one male was observed visiting a dense *Lantana* patch at about 1000 h, and then in another patch 150 m away after 30–40 minutes. Several individuals showed similar patterns throughout the two years of study. Occasional disturbance on forest edges (removal of some flower patches)

TABLE 2. Permanence of marked *H. erato phyllis* in the "Morro do Voturuá". Days elapsed between marking and last recapture represent the minimum permanence (MP) for each individual.

MP	Males	P(%)	Females	P(%)	Total
1–20	51	33.1	18	60.0	69
21–40	38	24.7	5	16.7	43
41–60	34	22.0	5	16.7	39
61–80	21	13.6	1	3.3	22
81–100	9	6.0	1	3.3	10
>100	1	0.6	0	0.0	1
Total	154	100.0	30	100.0	184

resulted in disappearance of some individuals from the study area for up to two weeks.

Four *Passiflora* species were recorded as larval food-plants in MV: *Passiflora alata* Dryand, *P. edulis* Sims (both used rarely), *P. jileki* Wawra, and *P. capsularis* L. Other species may be used in the same area and in the neighboring sites. The behaviors observed in ovipositing females and larvae were the same as reported in the literature (see Brown 1981).

## DISCUSSION

### Populational Ecology and Adult Biology

The population parameters of *H. erato phyllis* seen in this study agree with those reported for other tropical *Heliconius* (Turner 1971, Ehrlich & Gilbert 1973, Araujo 1980, Mallet & Jackson 1980, Ehrlich 1984, Mallet et al. 1987, Quintero 1988). The MV population was reasonably stable in numbers during the two years of study if compared with species of other sub-families such as Ithomiinae and Troidini, both showing pronounced fluctuations in numbers through time (Vasconcellos-Neto 1980, Brown et al. 1981, Francini 1989, Freitas 1993, 1996, Tyler et al. 1994, Pinto & Motta 1997). Other features observed for *H. erato* in the present study were the continual recruitment of new individuals, low density of adults, absence of sudden increases and decreases in numbers of individuals, and non-cyclical age structure. The population seems to be less affected by climate than those observed by Benson (1978) for populations in a drier site in Rio de Janeiro or Saalfeld and Araujo (1981) for populations

TABLE 3. Maximum distance (m) traveled by adults of *H. erato phyllis* in MV.

	Residents		Vagile	
	up to 50	51–150	150–500	>500
Males	39	17	77	3
Females	4	8	13	2
Total	43	25	90	5



TABLE 4. Frequency distributions, sample size (N), mean (X), and standard deviation (SD) of the number of "red raylets" for month of first capture in butterflies of both sexes captured in the "Morro do Voturua".

Month/year	Number of Red raylets							N	X $\pm$ SD
	1	2	3	4	5	6	7		
Aug/1994	2	5	2	8	2	1	0	20	3.3 $\pm$ 1.4
Sep/1994	0	3	6	4	2	0	0	15	3.3 $\pm$ 1.0
Winter/1994	2	8	8	12	4	1	0	35	3.3 $\pm$ 1.2
Oct/1994	0	0	4	1	3	0	0	8	3.9 $\pm$ 1.0
Nov/1994	0	2	6	6	4	3	0	21	4.0 $\pm$ 1.2
Dec/1994	0	2	7	2	5	1	0	17	3.7 $\pm$ 1.2
Spring/1994	0	4	17	9	12	4	0	46	3.9 $\pm$ 1.2
Jan/1995	0	4	8	5	10	6	0	33	4.2 $\pm$ 1.3
Feb/1995	1	0	0	1	2	5	0	9	5.0 $\pm$ 1.6
Mar/1995	1	0	3	4	8	3	1	20	4.5 $\pm$ 1.4
Summer/1995	2	4	11	10	20	14	1	62	4.4 $\pm$ 1.4
Apr/1995	0	0	1	0	5	3	1	9	5.3 $\pm$ 1.1
May/1995	1	2	3	3	8	0	0	17	3.9 $\pm$ 1.3
Jun/1995	0	2	3	4	5	2	0	16	4.1 $\pm$ 1.3
Autumn/1995	1	4	7	7	18	5	1	43	4.3 $\pm$ 1.3
Jul/1995	2	4	9	4	5	1	0	25	3.4 $\pm$ 1.3
Aug/1995	2	0	1	1	1	1	0	6	3.3 $\pm$ 2.1
Sep/1995	2	2	5	1	1	0	0	11	2.7 $\pm$ 1.2
Winter/1995	6	6	15	6	7	2	0	42	3.2 $\pm$ 1.4
Oct/1995	0	2	3	1	0	2	0	8	3.6 $\pm$ 1.6
Nov/1995	1	1	3	6	1	1	0	13	3.6 $\pm$ 1.6
Dec/1995	0	2	1	0	1	1	0	5	3.6 $\pm$ 1.8
Spring/1995	1	5	7	7	2	4	0	26	3.6 $\pm$ 1.4
Jan/1996	0	2	1	1	5	2	0	11	4.4 $\pm$ 1.4
Feb/1996	0	0	1	0	4	5	0	10	5.3 $\pm$ 1.0
Mar/1996	0	1	4	0	5	5	0	15	4.6 $\pm$ 1.4
Summer/1996	0	3	6	1	14	12	0	36	4.7 $\pm$ 1.3
Apr/1996	0	0	2	3	4	6	1	16	5.1 $\pm$ 1.2
May/1996	0	1	1	0	1	1	0	4	4.0 $\pm$ 1.2
Jun/1996	0	1	2	1	2	1	0	7	4.0 $\pm$ 1.4
Autumn/1996	0	2	5	4	7	8	1	27	4.6 $\pm$ 1.4
Jul/1996	1	3	2	1	2	0	0	9	3.0 $\pm$ 1.5
Aug/1996	0	1	0	0	0	2	0	3	4.7 $\pm$ 2.3
Sep/1996	2	3	3	0	0	0	0	8	2.2 $\pm$ 0.8
Winter/1996	3	7	5	1	2	2	0	20	2.9 $\pm$ 1.5
Total	15	43	81	57	86	52	3	337	3.9 $\pm$ 1.4

much farther south. In the latter populations, three distinct phases were reported: a period of rapid growth in early spring, a period of maximum density in summer through autumn, and an abrupt decline in winter (Saalfeld & Araujo 1981, Romanowsky et al. 1985). In the periods of maximum density, the number of individuals captured in these populations could be very high (more than 150 individuals reported in one roosting site) in relation to the maximum values obtained in the present study (from 20 to 30 individuals) (Saalfeld & Araujo 1981, Romanowsky et al. 1985).

The average time of residence and the life expectancy reported in the present study are both high, like those of other *Heliconius* (Turner 1971, Benson 1972, Ehrlich & Gilbert 1973, Araujo 1980, Quintero 1988), including the populations from southern Brazil (Romanowsky et al. 1985). The values are higher than those of many Ithomiinae, Pieridae, and Papilionidae

in the same or nearby sites (Table 5; see also Young & Moffett 1979, Vasconcellos-Neto 1980, Brown et al. 1981, Freitas 1993, 1996, Tyler et al. 1994, Pinto & Motta 1997). The high values for residence are not related to geographic location of the populations, since they are higher in *Heliconius erato* than in butterflies of other groups in the same and nearby sites (Table 5).

In part the high values of residence reported in *Heliconius* could be related to the movements and dispersal of the adults. Some *Heliconius* and *Eueides* butterflies are known to have restricted home ranges throughout their lives, and even if adults can fly distances up to 5 km within the forest (Brown 1981, Pansera & Araujo 1983, Romanowsky et al. 1985, Mallet et al. 1987), small areas of open field could act as efficient barriers to dispersal (Romanowsky et al. 1985). This pattern contrasts with that of "nomadic" butterflies such as Ithomiinae and Troidini (see discus-

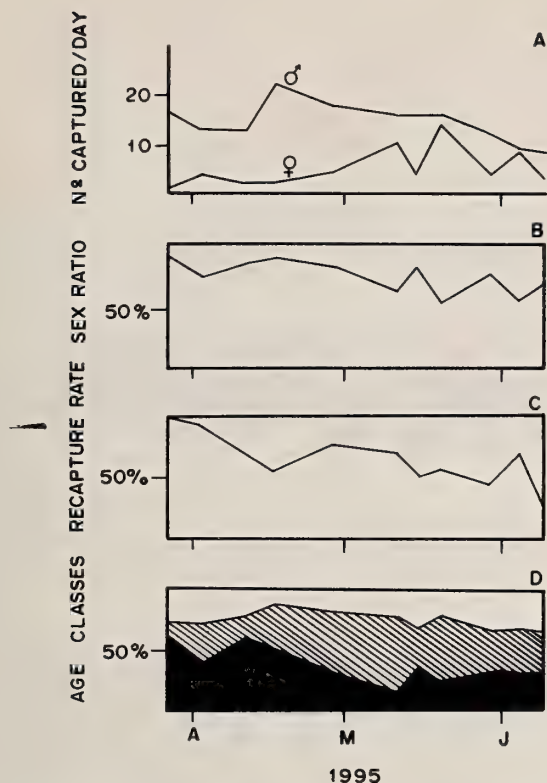


FIG. 6. Populational parameters of *H. erato phyllis* in Vale do Rio Quilombo, March to June 1995. A, daily captures of males (top line) and females; B, sex ratio as percent of males in each day's captures; C, percent of captures of males; D, age structure of males as in Fig. 4.

sion in Mallet et al. 1987) and probably other more primitive genera of Heliconiini like *Dryas*, *Agraulis* and *Dione* (K. Brown, pers. comm.). For example, although some Ithomiinae are reported to live as long as 10 months (e.g., *Mcclungia salonina* (Hewitson), R. S.

C. Dias & K. S. Brown, pers. comm.), several studies showed low rates of recapture and low permanence values for species in this subfamily, probably as a result of the high dispersal of the individuals (Gilbert 1993). But even if movement explains in part the residence values of adults, almost certainly the high actual longevity of the adults is the main factor affecting this parameter in *Heliconius*.

In the present study, sex ratio was male biased; several previous field studies reported male biased sex ratios even when the sex ratio in the laboratory was 1:1 (Ehrlich & Gilbert 1973, Mallet & Jackson 1980, Ehrlich 1984, Ehrlich et al. 1984, Freitas 1993). This difference in capture between sexes may be due to differential behavior of the adults, with males generally flying in the same places as the collectors, and females more dispersed throughout the habitat looking for host plants (Freitas 1996).

Contrasting with these features, which agree with those found in other species of *Heliconius*, the use of food resources by *H. erato phyllis* in the São Vicente region is unlike that of many other tropical species of the same genus. The butterflies seem to prefer feeding along forest edges on common second-growth flowers, even though a species of Rubiaceae and *Gurania* sp. (Cucurbitaceae) flowers are common in clearings in the forests, where they are heavily used by *Heliconius numata robigus* Weymer. It is interesting that sympatric *H. sara apseudes* (Hübner) and *H. ethilla narcaea* (Godart) have flower preferences similar to those of *H. erato phyllis* (pers. obs.), perhaps related to their specialization on small pollen grains (Boggs et al. 1981) and the use of larval host plant species typical of successional habitats (Gilbert 1991).

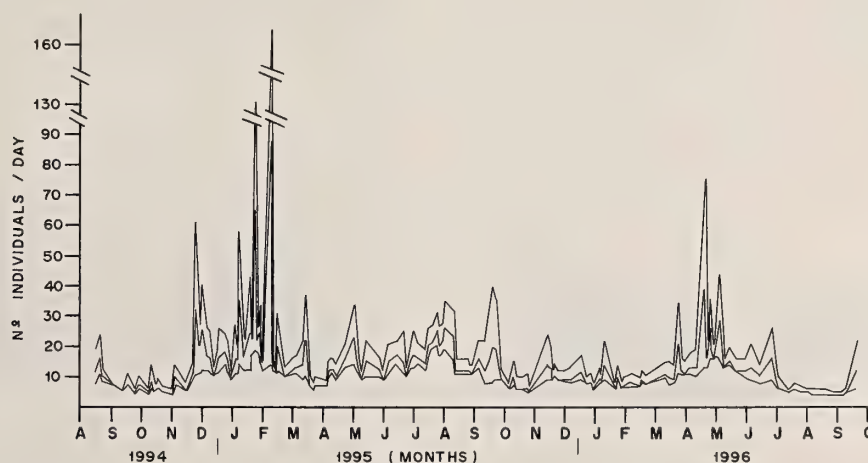


FIG. 7. Estimated population size (Jolly-Seber) for *H. erato phyllis* (males) in Morro do Voturuá, August 1994 to September 1996 (middle). The maximum number of individuals is given as the estimate plus the error (top line), and the minimum number is given as the NIPD (bottom line), assuming that the population could not be lower than this number (see also Freitas 1993, 1996).



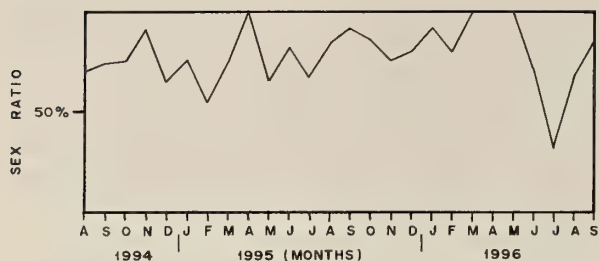


FIG. 8. Sex ratio for *H. erato phyllis* marked in Morro do Voturuá, August 1994 to September 1996 (based on monthly recruitment), as percent of males in each month's captures.

### Wing Color Pattern

Although the number of red basal spots is relatively constant in this population of *H. erato phyllis*, other elements of color pattern are not: the number of "red raylets" varies seasonally, and the shape of the red raylets and the cubital spot on the dorsal forewing vary during the year with no clear pattern. The number and shape of the basal spots on the ventral hindwing is one of the distinctive characters used in *Heliconius* classification. This character was discussed by Emsley (1965) as probably important in courtship as a recognition mechanism. If this is true, the constancy of this character is easily explained.

The pattern observed in the shape of the red raylets and in the cubital spot is not easy to explain, but random variation is the most probable hypothesis. There are no known pressures acting on these two characters.

Oliveira and Araujo (1992) proposed that the mean number of red raylets is related to temperature: the hot months should have a high proportion of individuals with numerous red raylets. The genetic determination of this character was defined by Pansera and Araujo (1983), but numeric polyphenism could not be discarded. Polyphenism occurs in several species in seasonal environments (Brakefield & Larsen 1984, Braby 1994, Windig et al. 1994). In southern Brazil (30°S), adult populations greatly decline during the

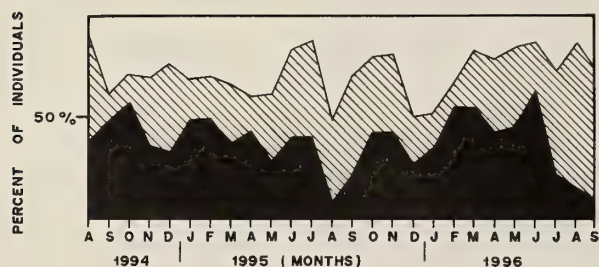


FIG. 9. Age structure for male *H. erato phyllis* in Morro do Voturuá, August 1994 to September 1996 (black = fresh individuals, hatched = intermediate, white = worn individuals as % of each day's captures).

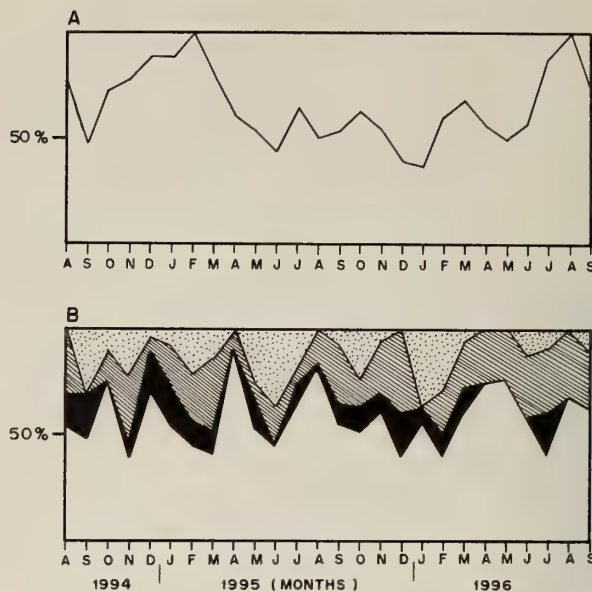


FIG. 10. Monthly variation of two wing pattern elements in adults of both sexes of *H. erato phyllis* in Morro do Voturuá, August 1994 to September 1996. A, ratio between red raylets of both shapes as percentage of individuals with red raylets shaped like dots. B, ratio among the four different phenotypes of the colored spot in the inner angle of space Cu1-Cu2: white = present yellow, black = present red, hatched = absent, dotted = fused with the subapical red macula.

cold winter, and the variation in the number of red raylets could be explained through the resulting bottlenecks (A. M. Araujo, pers. comm.). In the São Vicente region (24°S), low temperature does not kill adults in winter, and genes are not eliminated in this way. Although color pattern frequencies are not stable, the population itself shows a relative stability in number throughout the year, indicating that this variation occurs without reduction in population size, suggesting that the variation could be due to simple numerical polyphenism.

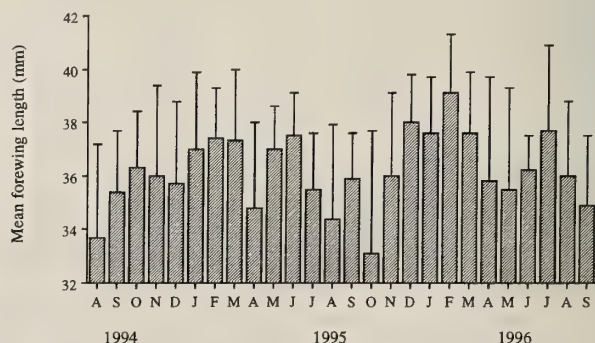


FIG. 11. Mean forewing length of males of *H. erato phyllis* in Morro do Voturuá, August 1994 to September 1996 (based on monthly recruitment). Histogram bars = monthly means, line extensions = standard deviation.

TABLE 5. Residence values (in days) for some butterfly species in Southeastern Brazil. Mean mr = mean minimum residence, mo = maximum for one individual.

	Males		Females	
	mean mr	mo	mean mr	mo
<b>São Vicente Region</b>				
<b>Nymphalidae</b>				
<i>Heliconius erato phyllis</i> <sup>1</sup> Morro do Voturuá	37.6 ± 25.8	127	22.6 ± 23.0	89
<i>Heliconius erato phyllis</i> <sup>1</sup> Morro do Japuí	18.04 ± 14.6	47	—	22
<i>Melinara ludovica paraiya</i> Reakirt <sup>2</sup>	14.1 ± 14.1	55	—	—
<i>Melinara ethra</i> Godart <sup>2</sup>	13.7 ± 12.9	47	—	—
<i>Placidula euryanassa</i> <sup>2,3</sup>	8.4 ± 8.3	45	7.2 ± 5.7	23
<i>Mechanitis lysimnia lysimnia</i> Fabricius <sup>2</sup>	15.5 ± 15.4	67	18.3 ± 16.2	72
<i>Dircenna dero celtina</i> Burmeister <sup>2</sup>	9.4 ± 6.9	23	10.9 ± 10.5	49
<i>Heterosais edessa</i> Hewitson <sup>2</sup>	12.9 ± 15.1	65	13.5 ± 10.3	39
<i>Hypothyris ninonia daeta</i> (Boisduval) <sup>4</sup>	16.3 ± 11.1	40	14.2 ± 16.2	52
<i>Pseudoscada erruca</i> (Hewitson) <sup>4</sup>	9.9 ± 9.6	25	—	33
<i>Ithomia drymo</i> Hübner <sup>4</sup>	7.0 ± 7.3	17	12.3 ± 12.1	26
<i>Actinote pellenaea pellenaea</i> Hübner <sup>5</sup>	3.2 ± 2.6	12	—	6
<i>Actinote brylla</i> Oberthür <sup>5</sup>	—	16	—	16
<b>Papilionidae</b>				
<i>Parides anchises nephalion</i> Godart <sup>6</sup>	14.1 ± 8.2	30	9.0 ± 3.6	12
<b>Other regions</b>				
<b>Nymphalidae</b>				
<i>Heliconius erato phyllis</i> <sup>7</sup>	30.7 ± 29.0	112	—	—
<i>Aeria olena olena</i> Weymer <sup>8</sup>	8.7 ± 5.9	24	11.7 ± 2.5	14
<i>Actinote zikani</i> D'Almeida <sup>9</sup>	3.9 ± 1.3	7	—	—
<i>Pierella lamia</i> Sulzer <sup>10</sup>	—	60	—	—
<b>Pieridae</b>				
<i>Eurema elathea</i> (Cramer) <sup>11</sup> dry season	10.9 ± 9.1	52	9.7 ± 9.8	54
<i>Eurema elathea</i> <sup>11</sup> wet season	8.8 ± 5.6	28	6.9 ± 4.2	21

Superscript numbers : 1, this study; 2, Freitas 1996; 3, Freitas 1993; 4, Freitas, unpubl. data from Morro do Japuí; 5, Francini 1989; 6, Freitas, unpubl. data from Morro do Voturuá; 7, Francini, unpubl. data from Lavras, MG, Brazil; 8, Vanini and Freitas, unpubl. data from Campinas, SP; 9, Francini, unpubl. data from Paranaipiacaba, SP; 10, Freitas, unpubl. data from Sete Barras, SP; 11 Vanini, Bonato and Freitas, unpubl. results from Campinas, SP.

### Ecological Plasticity in *Heliconius*?

Several features of *H. erato* vary in different parts of the neotropics. Although in the São Vicente region and Trinidad the populations are stable, maintaining constant low numbers throughout time (Turner 1971, R. B. Francini, pers. obs.; this study), in southern Brazil they show strong fluctuations over the year, with some extinction in colder years (Saalfeld & Araujo 1981, Romanowsky et al. 1985). *Heliconius erato* is reported as feeding on more than 37 species and 6 genera/subgenera of Passifloraceae (Benson et al. 1976, Brown 1981, Spencer 1988), even using *Passiflora edulis* and *P. alata*, host species normally rejected in most populations, on forest edges and urban areas (this study, A. V. L. Freitas, pers. obs., and unpublished results by L. S. Otero and K. S. Brown Jr.). The differences in use of flower resources among areas in this study shows that *H. erato phyllis* rapidly responds to variations in resource availability in different sites and seasons.

*Heliconius erato*, especially the subspecies *phyllis*, seems to be able to persist in many kinds of climate

and vegetation. Colonies of this subspecies are present in virtually any kind of vegetation in southeastern and southern Brazil, including primary and secondary forest edges, urban parks, plantations of *Pinus* and *Eucalyptus*, riparian forests, savannas and sandy soil forests, and in tropical, subtropical, and temperate environments (Araujo 1980 and pers. obs. of the authors). This is probably related to the ability of this species (especially the subspecies *phyllis*) to use a great range of larval and adult resources, and change behavior and preferences according to the environment (=ecological plasticity).

Such statements could apply not only to *H. erato*, but also to *H. sara* and *H. ethilla* populations in southeastern and southern Brazil, both with similar generalist habits, and could help to explain patterns of distribution of the species of this genus. In contrast to the three species cited above, four other *Heliconius* of southeastern Brazil have much more restricted habits. *Heliconius melpomene nanna* Stichel, *H. numata robigus* and *H. nattereri* Felder & Felder, are restricted to limited sectors of forest habitats, the last one with a



very small range, a poor competitor with *H. sara* and other lowland species (Brown 1972, W. W. Benson, pers. comm.); *H. besckei* Ménétriés (a co-mimic of *H. erato*) is typical of Atlantic forest mountains, in primary and secondary forests at medium high altitudes, descending to sea level only in winter (Brown & Mielke 1972 and unpublished results by the authors).

Even though environmental tolerance may help explain distributions of the species of *Heliconius*, other factors need to be investigated. Benson (1978) argues that the availability of new host plant shoots in the dry winter results in high competition and is responsible for the absence of *H. melpomene* in a seasonal site in South Brazil. In the São Vicente region, however, this seasonality is much less pronounced, and periods of severe drought are virtually absent (Fig. 2); new shoots of *Passiflora* species seem to be abundant throughout the year, and though a detailed study needs to be carried out, this could not explain the absence of *H. melpomene* south of Rio de Janeiro State. Although these ideas and many others were discussed by Gilbert (1984), there still seem to be more questions than answers.

Population studies need to be undertaken with other species of Heliconiini, especially the more widespread species of *Heliconius*, such as *H. ethilla* and *H. sara*. The presence of seasonal polyphenism may indicate species with broad tolerances to different environments, as has been suggested for other polyphenic butterflies (Shapiro 1976, Kingsolver & Wiernasz 1991, Van Dyck et al. 1997), although in *Heliconius* this could be apparently without adaptive consequences. These studies could guide future research in population biology of butterflies, and help in the understanding of the ecology of tropical insects.

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## A HOSTPLANT-INDUCED LARVAL POLYPHENISM IN *HYALOPHORA EURYALUS* (SATURNIIDAE)

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**ABSTRACT.** A hostplant-induced larval polyphenism is described in *Hyalophora euryalus*. Larvae reared on madrone (*Arbutus menziesii*) and manzanita (*Arctostaphylos patula*) have greatly reduced or no lateral nor abdominal scoli; sibs reared on the conifer Douglas-fir (*Pseudotsuga menziesii*) possess fully expressed scoli. Other native hosts (*Ceanothus integerrimus* and *Prunus emarginata*) do not induce the polyphenism. The third instar appears to be the critical stage during which the polyphenism is determined. Size and fecundity of adults reared on madrone and Douglas-fir are comparable. The evolutionary basis of this polyphenism is discussed in terms of increased crypsis on the appropriate host. Madrone may be an ancestral host, a member of the Madro-Tertiary flora with which *H. euryalus* is closely associated. Douglas-fir may have been important during the re-invasion of northern and boreal regions following the Pleistocene. Mature larvae of the allied *Callosamia* also have a similar "nude" larval phenotype, suggesting a possible ancestral genetic potential to evolve the polyphenism.

**Additional key words:** caterpillar, crypsis, developmental plasticity, life cycle, phenotypic plasticity, polymorphism.

Although known as the "Ceanothus silk moth", *Hyalophora euryalus* (Boisduval) is polyphagous and occupies an unusual range of West Coast plant communities including the deserts of Baja California, Coast Range and Sierran chaparral, Central Valley riparian habitat, Great Basin scrub, and conifer forests in the Sierra Nevada and the Cascades (Tuskes et al. 1996). In the central Sierra Nevada the larvae feed on at least eight genera of shrubs and trees, representing six plant families, including the conifer Douglas-fir (*Pseudotsuga menziesii* Mirb. [Franco]). By dispersing their populations over a range of plant communities, hostplant generalists may benefit from reduced search time for ovipositing females, and partially escape from predators and parasitoids associated with specific plant species or plant communities (Janzen 1984a). Nevertheless, a large, palatable larva like *H. euryalus* must also depend on crypsis to survive. Its larval phenotype inevitably represents a compromise in camouflage value among such a wide variety of foliage shapes, colors, and lighting regimes. The host-induced larval polyphenism reported here appears to represent an evolutionary response to this dilemma.

The larvae of *H. euryalus* differ from congeners in the last two instars in the tendency of scoli to be smaller relative to total larval size, and in being armed with fewer and smaller spines on their scoli (Fig. 1) (Collins 1997, Tuskes et al. 1996). This trend reaches its extreme expression in a "nude" fifth instar larval phenotype in which all but the two pairs of dorsal thoracic scoli, the first dorsal abdominal pair, and the caudal scoli are very reduced or absent. I have observed this phenotype in approximately a third of wild collected larvae in the central Sierra Nevada, and have recorded it in populations from as far north as Victoria, British

Columbia and as far south as Baja California. No other *Hyalophora* taxon expresses this reduction in scoli.

The environmental control of scoli expression was discovered fortuitously when I divided a batch of *H. euryalus* ova laid by a single female into two lots, one of which I reared on *Arbutus menziesii* Pursh (madrone; Ericaceae) and the other on *Pseudotsuga menziesii* (Douglas-fir; Pinaceae). Both are common hosts for *H. euryalus* throughout the Sierra Nevada and Cascade Range. All larvae on madrone developed into the nude morph (Fig. 2), while their sibs on Douglas-fir all expressed fully developed scoli (Fig. 3). In this paper I report the results of a controlled breeding program to verify these findings and to further investigate the genetic basis for this host-induced polyphenism. In the discussion I offer the interpretation that the nude larval morph is especially cryptic on madrone and the full expression of scoli is cryptic on Douglas-fir.

### MATERIALS AND METHODS

Stock of *Hyalophora euryalus* from northern California was derived from a female collected as a cocoon near Donner Lake, Placer Co., and mated to a wild male from Nevada Co. Subsequent generations were produced by mating reared females to wild Nevada Co. males. One other brood resulted from mating a reared female from Victoria, British Columbia, Canada, stock to a wild male from Nevada Co., California. Ova were obtained by confining females in paper bags and cutting out sections with clusters of ova attached. Ova were incubated during May in a screened-in insectary at 1000 meters in Nevada Co., California. Newly eclosed larvae were confined with twigs of hostplant in 15 cm × 4 cm plastic petri dishes. After 2 to 3 days larvae were transferred to nylon mesh sleeves placed on *Arbutus menziesii*, *Pseudotsuga menziesii*, and other indigenous hosts. Larval growth

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FIG. 1. *Hyalophora euryalus* fifth instar reared on *Ceanothus integrerrimus*; most common phenotype in mid-latitude California Sierra Nevada, with reduced, but entire, scoli. FIG. 2. Fifth instar *H. euryalus* of the "nude" phenotype reared on *Arbutus menziesii* (madrone). Dorsal and lateral abdominal scoli reduced to near absence. FIG. 3. Fifth instar *H. euryalus* reared on *Pseudotsuga menziesii* (Douglas-fir) with fully developed scoli, induced by feeding on this host. FIG. 4. Fifth instar *H. euryalus* reared on *Arctostaphylos patula* (manzanita), which induces the "nude" phenotype. Siblings of larva in Fig. 3.

and phenotypes expressed were monitored periodically under these natural conditions. Fifth instar larval phenotypes were scored as a presence or absence of abdominal scoli. For larvae reared on *Arbutus* or *Arctostaphylos* (manzanita) compared to *Pseudotsuga* this was virtually a qualitative trait, although some larvae expressed much reduced button-like scoli. Larval morph scores were analyzed using a Chi-square test,

assuming a null hypothesis that a simple polymorphism existed based on a single major genetic locus, independent of hostplant.

The possible effect of the maternal hostplant was tested by mating a female reared on *Pseudotsuga* and another on *Arbutus* each to wild males, and rearing larvae from both matings as split broods on both hosts as before.



TABLE 1. Effect of hostplant on expression of fifth instar larval scoli in *Hyalophora euryalus*.

Brood ♀ × ♂	<i>Pseudotsuga</i>		<i>Arbutus</i>	
	scoli	nude	scoli	nude
Victoria, B.C. × Nevada Co., Calif. 1994	26	0	0	25
Donner L., Placer Co. × Nevada Co., Calif. 1996	23	0	1	22
Sib above × Nevada Co. 1997a	7	0	0	2
As above 1997b	9	0	0	13
Total:	65	0	1	63

Chi<sup>2</sup> for pooled data = 128.0 .0005 >> p.

To assess the possible effect of hostplant species on reproductive fitness, fecundity of females was recorded for *Pseudotsuga* vs. *Arbutus* and compared to published data for other hosts. Since saturniid females eclose with a full complement of mature ova and oviposit virtually all their ova, the total number of eggs laid yields a direct index of fecundity when divided by forewing length to standardize for variation in adult size (Collins 1997). Unmated females were dissected to determine fecundity.

In an attempt to determine the critical instar in which induction of larval morph occurs, I initially switched one batch of 20 third instar larvae from *Arbutus* to *Pseudotsuga*. All larvae died within a few days of transfer, apparently from either refusing to feed on or an inability to metabolize this new host. This test was repeated in 1998 with lots of ten sibling larvae each reared in cages on either *Pseudotsuga* or *Arbutus*, then switched to the other hostplant of the pair during the third instar. A control lot was reared continuously on the common foothill host, *Ceanothus integerrimus*. In addition, a fourth lot was reared on *Ceanothus* until the third instar, and then switched to *Pseudotsuga*. Individuals from a different brood were reared on *Prunus emarginata* (Rosaceae).

TABLE 2. Effect of maternal parental hostplant on induction of larval morph in *Hyalophora euryalus*. Siblings of 1997 broods in Table 1.

Host	Female parental host			
	<i>Pseudotsuga</i>		<i>Arbutus</i>	
	scoli	nude	scoli	nude
<i>Arbutus</i>	0	13	0	2
<i>Arctostaphylos</i>	0	14	0	9
<i>Pseudotsuga</i>	7	0	9	0

TABLE 3. Phenotype and survival of *Hyalophora euryalus* sibling larvae switched to new host as third instars.

Host switch	No. switched as 3rd instar	Number survived	Fifth instar phenotype		
			full scoli	intermediate*	nude
1998a: ♀ progeny of 1997a × wild Nevada Co. ♂					
<i>Arbutus</i> - <i>Pseudotsuga</i>	4	4	4	0	0
<i>Ceanothus</i> - <i>Pseudotsuga</i>	5	4	2	1	1
<i>Pseudotsuga</i> - <i>Arbutus</i>	8	3	0	1	2
<i>Ceanothus integerrimus</i> (Control, not switched)	7	7	3	0	4
1998b: ♀ progeny 1997a × sib. Sleeved as ova on live hostplant, not switched.					
<i>Prunus emarginata</i>			2	9	13
<i>Arctostaphylos patula</i>			0	0	13
<i>Pseudotsuga menzeisii</i>			6	0	0
* Larvae with the intermediate phenotype possessed entire but reduced lateral scoli, and no or only remnant dorsal abdominal scoli.					

\* Larvae with the intermediate phenotype possessed entire but reduced lateral scoli, and no or only remnant dorsal abdominal scoli.

## RESULTS

Larval phenotypes for broods reared on *Pseudotsuga* vs. *Arbutus* are shown in Table 1. A nearly complete dichotomy in phenotypes for both broods was seen in relation to hostplant, disproving the null hypothesis that the expression of scoli reduction is due to a simple genetic polymorphism independent of hostplant.

During the first two rearing seasons, survival on both hostplants was nearly 100%. In 1997 larvae in some sleeves suffered heavy parasitism by the braconid *Cotesia*. Although exact data were not collected, I observed that larval growth rates on *Arbutus* were consistently faster in all broods than those for larvae reared on *Pseudotsuga*. Notes on approximate average time to cocoon spinning show that larvae on madrone matured about one week to 10 days faster than on Douglas-fir.

No effect of maternal hostplant on larval phenotype was seen (Table 2), as larval morphs showed the expected dichotomy regardless of the hostplant of the female parent. In addition, larvae reared on *Arctostaphylos* completely expressed the nude phenotype in the last instar (Table 2, Fig. 4). Observation of larvae showed that the reduction of scoli was nearly as pronounced in the fourth instar on *Arbutus* and *Arctostaphylos*, although the majority possessed scoli as small knobs, especially the lateral rows. In all broods, third instars possessed fully developed scoli. However, of six third instar larvae reared in 1997 on *Pseudotsuga*, three had all scoli heavily pigmented with black,

TABLE 4. Effect of hostplant on fecundity. Index = no. ova/forewing length.

No. ova	Forewing length	Index
<i>Arbutus</i>		
California: Placer Co. × Nevada Co.		
228	55	4.15
130	57	2.28
151	57	2.65
Canada, Victoria B.C. × California, Nevada Co.		
143	57	2.51
Avg.		
163.0	56.5	2.90
<i>Pseudotsuga</i>		
California: Placer Co. × Nevada Co.		
247	60	4.12
192	62	3.10
154	55	2.80
Canada, Victoria B.C. × California, Nevada Co.		
178	57	3.12
209	59	3.54
Avg.		
196.0	58.6	3.34
<i>Prunus emarginata</i>		
California, Nevada Co.; avg. 12 pairings (Collins 1997)		
175	58.3	2.99
<i>Ceanothus integerrimus</i>		
California, Nevada Co.		
179	57	3.14

as is seen in *Hyalophora columbia columbia* and *Hyalophora columbia gloveri*, while the remaining three possessed yellow dorsal and light blue lateral scoli as is typical of *H. euryalus* (Tuskes et al. 1996). Of 15 third instars examined in madrone broods, none possessed black scoli, nor were such dark forms seen among madrone broods in previous seasons, although careful notes were not made previously on third instar coloration. In 1998 among third instar larvae on *Pseudotsuga* two possessed black lateral scoli with yellow dorsal scoli, three had blue tipped with black lateral scoli and yellow dorsal scoli, none were all black, and two had the normal blue lateral and yellow dorsal scoli coloration. All ten third instar larvae on madrone possessed the yellow and blue pattern.

The effects of host-switching on survival and larval phenotype are shown in Table 3. Initial losses from the

lots of 10 neonates were highest in the lot begun on *Arbutus*, due apparently to wandering off the host-plant. Only 2 larvae were lost before the third instar for those begun on *Pseudotsuga*. None of the controls on *Ceanothus* was lost. After host switching, the lot switched from *Pseudotsuga* to *Arbutus* suffered the greatest loss with only 3 of 8 surviving. Larvae switched from *Arbutus* to *Pseudotsuga* expressed fully developed scoli. However, larvae switched from *Ceanothus* to *Pseudotsuga* showed different phenotypes: one larva was intermediate with small but distinct lateral scoli and very reduced or absent dorsal scoli; two other fifth instar larvae had large scoli and one was of the nude phenotype. Of the larvae switched from *Pseudotsuga* to *Arbutus* two expressed the nude phenotype but one other was intermediate. Control larvae reared continuously on *Ceanothus* displayed both morphs; some had fully developed scoli, while others had the nude morph.

The brood reared on *Prunus emarginata* (Table 3) also expressed all three larval morphs in the final instar, while siblings reared on *Arctostaphylos* and *Pseudotsuga* expressed the expected nude vs. scoli phenotypes. These results suggest that *Prunus emarginata* and *Ceanothus integerrimus* are neutral with respect to the host-induced polyphenism.

The host switching experiments suggest that the third instar is the stage that is responsive to host cues, thus controlling final instar phenotype, because exposure during the first two instars can be counteracted by subsequent exposure to other hostplant taxa. Although I did not attempt to subject fourth instars to host switching, casual observations showed that the fourth instar phenotype was usually an accurate predictor of final instar phenotype. Fourth instars with very reduced scoli often produced nude fifth instars. However, two fourth instars reared on *Prunus* and possessing fully developed scoli changed to the nude phenotype in the fifth instar.

Sibling females reared on *Pseudotsuga* or *Arbutus* did not differ in fecundity (Table 4). Average number of ova laid, forewing length, and fecundity index were larger for those reared on *Pseudotsuga*, although the sample size was too small to justify calculating statistical significance. Collins (1997) reported an average and SD for these parameters, respectively, of  $175.5 \pm 36.8$ ,  $58.3 \pm 4.6$ ,  $2.99 \pm 0.48$  for a sample of 12 *H. euryalus* reared on *Prunus emarginata*.

#### DISCUSSION

In discussing the evolutionary significance of larval phenotypic plasticity in *H. euryalus*, it is important to distinguish between the terms polymorphism and polyphenism. In a polymorphism, genetic differences among



individuals produce discrete phenotypes. A polymorphism is a population phenomenon; the frequency of alternate morphs in the population reflects the frequency of those genes controlling the expression of each morph, and the phenotype of a given individual is dependent on its genotype. A polyphenism is the expression of a specific phenotype in response to environmental cues, which regulate gene action through a neural-molecular pathway. ("Phenotypic plasticity" is also a widely used term (Stearns 1989), although Williams (1992) objects to its non-genetic connotation). Every individual in a polyphenic population theoretically could be genetically identical for the loci in question, and phenotypic variation within the population then would be a consequence of individual exposure to variable environmental cues. In a seasonal polyphenism, immatures in the population respond to a reliable seasonal cue, such as photoperiod, to produce "spring" and "summer" adult phenotypes in pierids (Shapiro 1989) or in the saturniid genus *Actias* (Miyata 1974, 1986); or the "wet" and "dry" seasonal forms of the neotropical saturniid *Rothschildia lebeau* (Janzen 1984b), and in the African butterfly *Bicyclus* (Windig et al. 1994).

Fewer cases of larval polyphenism in Lepidoptera have been carefully documented. Greene (1989) showed that strikingly different cryptic phenotypes are produced in the geometrid *Nemoris* when larvae feed on oak flower buds in the spring versus leaves during the summer rainy season in southeast Arizona. Fink (1995) demonstrated that hostplant partly controls a color polyphenism in *Eumorphia* (Sphingidae) larvae, but was unable to do controlled breeding experiments due to the difficulty of pairing these moths in the lab. The number and spacing of the large, silvery, lancet-shaped scoli of certain Southwestern *Sphingicampa* (Saturniidae) appear to be influenced by hostplant leaflet size and number (Tuskes et al. 1996; P. Tuskes, pers. comm.). Plant secondary compounds may act as cues in controlling these polyphenisms, although a pupal color polyphenism in certain *Papilio* is controlled by light level and other environmental cues (West 1995, Sims & Shapiro 1983).

My interpretation of the nude larval morph in *H. euryalus* is that this phenotype is more cryptic on madrone than the morph with fully developed scoli. The leaves of madrone are large, typically 10–14 cm in length, with entire margins, and light grey-green below. Especially when viewed from below, even the mature larva of *H. euryalus* is inconspicuous in the nude morph as it rests or feeds underneath the large, similarly colored madrone leaf. The same argument can be applied to the association with *Arctostaphylos*; the leaves of most species are also glaucous with smooth,

entire margins, but smaller than the foliage of *Arbutus*. By contrast, the larval morph with fully developed scoli appears more cryptic against the foliage of Douglas-fir because the numerous scoli break up the solid mass and match the visual effect of spots of light shining through a matrix of small needles. In both cases, the cryptic appearance is lost when each morph is viewed against the foliage of the "inappropriate" hostplant. The trend in early instars of darkening of scoli seen in broods reared on Douglas-fir would seem to camouflage these larvae against the dark twigs and foliage of Douglas-fir. The early instars of the *Larix* feeder, *H. c. columbia*, are always black.

The larvae of the related *Callosamia* also have very reduced scoli in later instars (Tuskes et al. 1996). This condition is most pronounced in the Magnoliaceae specialists, *C. angulifera* and *C. securifera*, whose larvae are very cryptic hidden under the large leaves of their hostplants.

The foliage of *Pseudotsuga*, in common with other conifers, is rich in terpenes and so presents a metabolic barrier against some insect herbivores (Smith 1989, Gershenzon & Croteau 1991, Harborne 1997). In a study of Lepidoptera diversity associated with *Abies* and *Pseudotsuga*, Powell and De Benedictis (1995) list 40 species, of which 73% are conifer specialists. Conifer feeding is not common within the three North American saturniid subfamilies. The few known examples, with the exception of *Hyalophora euryalus*, are generally feeders on *Pinus* spp., whose congeners feed on leafy shrubs and trees (Lemaire 1988, Tuskes et al. 1996, Wolfe 1993). *Hyalophora euryalus* is exceptional because it is primarily a generalist on shrubs and trees, and also because it was the only species found on Douglas-fir that preferred older needles (Powell & De Benedictis 1995). My work confirms this preference. First year conifer needles have been shown to contain up to ten times the diterpene acids of older needles (Ohigashi et al. 1981), so feeding on older needles may be due to an avoidance of high levels of these diterpene acids.

Adaptation to a new host involves many complex fitness tradeoffs affecting the evolution of life history traits (Fox & Morrow 1981; Krainacker et al. 1987; Fox & Caldwell 1994; Leclaire & Brandl 1994). Although it is difficult to measure the metabolic and other "costs" of conifer feeding in *H. euryalus*, larvae on *Pseudotsuga* consistently matured more slowly than sibs reared on *Arbutus* and one larval brood begun on *Arbutus* could not switch to *Pseudotsuga* in the third instar. It is not known if this result was due to a refusal to initiate feeding, or perhaps due to the failure of induction of the synthesis of a critical enzyme (cf



Brattsten et al. 1977, Brattsten 1983; Moldenke et al. 1983). No reduction in adult size nor female fecundity was found in broods reared on *Pseudotsuga*.

The foliage of *Arbutus menziesii* may also contain secondary compounds exacting a metabolic cost from insect herbivores. Ezcurra et al. (1987) list cardiac glycosides, quinones, and tannins among others in leaves of the Mexican madrone species, *Arbutus xalapensis*. Larvae of *H. euryalus* switched from Douglas-fir to madrone were reluctant to accept madrone (Table 3).

Larvae feeding in the Douglas-fir canopy may partially escape those predators and parasites normally associated with the smaller trees and shrubs that serve as *Hyalophora* hosts. The majority of the Lepidoptera fauna feeding on Douglas-fir are microlepidoptera (Powell & De Benedictis 1995), which could attract a different set of predators and parasites than those attacking *Hyalophora*.

Danks (1994) asserts that genetic polymorphisms tend to evolve in predictable environments, while polyphenisms are associated with unpredictable environments. An example of a polymorphism in a predictable environment would be the various color forms of *Saturnia mendocino* larvae, which match the living green foliage and persistent yellow and mauve dead leaves all reliably present on manzanita (Tuskes et al. 1996). The array of hosts utilized by populations of *H. euryalus* represent an unpredictable environment. One can theorize that if a *H. euryalus* population were genetically polymorphic for larval scoli size, females ovipositing on both madrone and Douglas-fir would produce many larvae of the inappropriate phenotype, stranded on large trees against a non-cryptic background.

Collins (1997) proposes that conifer feeding in *Hyalophora* arose as an adaptation to post-Pleistocene environments, in which pioneer populations of *H. euryalus* fed on *Pseudotsuga* as they reinvaded northern and montane portions of the moth's current range, and *H. columbia columbia* similarly adapted to *Larix* (tamarack) as it spread north and east where it currently occurs in tamarack bogs. Even coastal populations of *H. euryalus* in southern California may accept and mature on *Pseudotsuga*, but the Rocky Mountain subspecies *H. c. gloveri* lacks this adaptation (Tuskes et al. 1996). Madrone and manzanita are members of the Madro-Tertiary flora, and probably represent ancestral *Hyalophora* hosts, based on comparative biogeographical evidence and the close association of *H. euryalus* with modern derivatives of this ancient flora (Collins 1997).

Fully developed fifth instar scoli appears to be the primitive condition in the Saturniidae (Ferguson 1971,

Minet 1994), and fifth instar scoli are prominently expressed in all *Hyalophora* taxa except *H. euryalus*. The neutral condition in *H. euryalus* is one of variable but reduced scoli in later instars. The evolution of the larval polyphenism in *H. euryalus* may best be described as the host-induced shift in this neutral developmental state toward either suppression of scoli when larvae feed on certain Ericaceae, or a shift in the opposite direction toward full scoli expression in larvae feeding on *Pseudotsuga*. Certain other hosts, such as *Ceanothus integerrimus* and *Prunus emarginata*, appear neutral in inducing the scoli polyphenism and a range of developmental variation in scoli expression occurs among siblings reared on these hosts. It is difficult to determine to what extent this represents genetic variation in loci controlling scoli development, given the environmental influence seen in this study, but I have observed larvae with fully developed scoli on *Arctostaphylos* (fig. 1d in Collins 1997).

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## A NEW *HYPATOPA* FROM COSTA RICA (GELECHIOIDEA: COLEOPHORIDAE: BLASTOBASINAE)

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**ABSTRACT.** *Hypatopa tapadulcea* is described from northwestern Costa Rica. A photograph of the imago and illustrations of wing venation and male and female genitalia are provided.

**Additional key words:** Lepidoptera, Blastobasini, Guanacaste, Puntarenas.

About ten years ago a survey of all Costa Rican fauna and flora was undertaken by Instituto Nacional de Biodiversidad (INBio). Among the many organisms collected were microlepidoptera, and through the efforts of Costa Rican “parataxonomists”, a large number of specimens of Blastobasinae have accumulated. Through the combined work of many Costa Ricans and invited scientists, an inventory for this neotropical region is possible. This paper describes *Hypatopa tapadulcea*, and represents one small work among several major studies planned by the author to make known the rich diversity of this group of moths.

Members of the Blastobasinae are generally small to medium-sized, drab moths with fewer than 150 species described worldwide. This number, however, greatly underestimates the species richness, as there are hundreds of undescribed species represented in collections, especially from the Neotropics.

Meyrick (1894) was the first to recognize the Blastobasinae as a monophyletic group. Recent studies by Adamski and Brown (1989) and Hodges (1998) have corroborated this notion, and have established monophyletic groupings at the generic and familial levels within the Blastobasinae and Gelechioidea, respectively.

Kornerup and Wanscher (1978) is used as a color standard for the description of the adult vestiture. Genitalia were dissected as described by Clarke (1941), except mercurochrome and chlorazol black were used as stains. Pinned specimens and genital preparations were examined with dissecting and compound microscopes. Measurements of wings and genitalia were made using a calibrated ocular micrometer.

### *Hypatopa tapadulcea* Adamski, new species

(Figs. 1–4)

**Diagnosis.** Male with inner margin of gnathos slightly widened, forming a small broadened lobe, sacculus subrectangular, aedeagus bulbous at base; female with ostium elongate, ductus seminalis wide at base, ductus bursae spiralled.

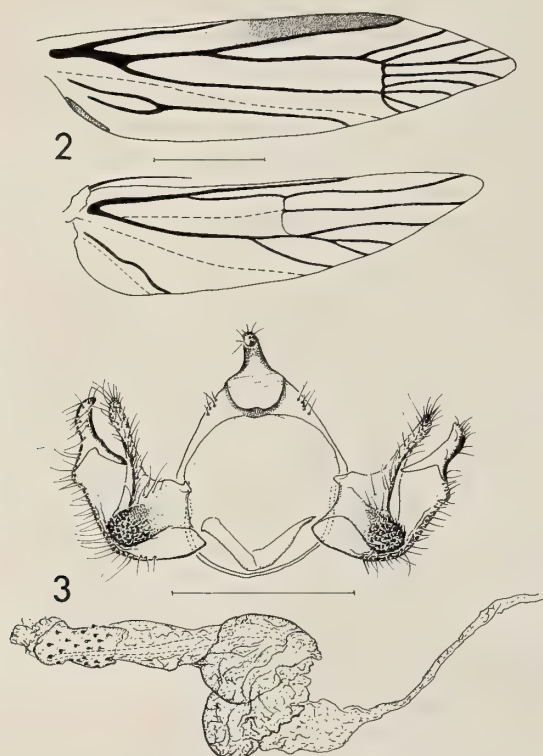
**Description.** *Head:* vertex and frontoclypeus with grayish-brown scales tipped with yellowish brown, females mostly pale yellow brown; outer surface of labial palpus with grayish-brown scales tipped with yellowish brown intermixed with grayish-brown scales, and grayish-brown scales tipped with pale grayish brown, and yellowish-brown scales, inner surface mostly with yellowish-brown scales intermixed with few grayish-brown scales; some males with inner surface patterned similar to outer surface; females with mostly yellowish-brown scales on both surfaces; antennal scape and pedicel patterned as above; flagellum mostly brownish gray intermixed with few yellowish-brown scales; proboscis pale yellowish brown. *Thorax:* basal area of tegula and mesoscutum grayish brown, pale grayish brown distally. Legs with outer surface mostly brown intermixed with few yellowish-brown scales, yellowish-brown bands near midtibia, apices of femur, tibia, and tarsomeres, undersurface with mostly pale yellowish-brown scales intermixed with few brown scales. *Forewing* (Fig. 1): length 5.1–6.5 mm ( $n = 77$ ), ground color yellowish brown intermixed with few brown scales; base posterior to CuP with a short dark-brown marginal streak; median fascia present, absent, or incomplete, usually distal 2/3 of wing darker than basal 1/3; discal spots absent; several similar-sized marginal brown spots on subapical and apical areas forming an irregular pattern; undersurface brown. Female paler than male. *Venation* (Fig. 2), cubitus 4-branched with  $M_2$  and  $M_3$  separate from  $M_1$ ,  $CuA_2$  about 45 degree angle to margin; distal part of  $M_1$  near parallel with  $M_2$  and  $M_3$ . *Hindwing:* brownish gray, females paler. *Venation* (Fig. 2), cubitus appearing 4-branched with  $CuA_1$  and  $M_3$  stalked beyond base of  $M_2$ . *Abdomen:* brownish gray above, pale yellowish brown beneath, male with pale yellowish-brown scales on digitate process of upper part of valva, female pale yellowish brown beneath. *Male genitalia* (Fig. 3): uncus slightly broadened at base, narrowed distally, apical part hooked posteriorly, apex rounded and sparsely setose; gnathos medially narrowed, medially widened, forming a small broadened lobe; tergal setae present; vin-





FIG. 1. Holotype of *Hypatopa tapadulcea* Adamski.

culum a thin band; juxta entire, not divided; lower part of valva with marginal setae, distal part setose, tapered to a pointed apex; upper part of valva with a subrectangular sacculus; sacculus with mostly stout setae intermixed with hairlike setae, a small cluster of microtrichia near outer margin at base of long, setose digitate process; aedeagus bulbous at base, parallel sided to apex; anellus setose. *Female genitalia* (Fig. 4): ovipositor telescopic, in four membranous subdivisions; ostium elongate, delimited within membrane



FIGS. 2-3. Wing venation and male genitalia of *Hypatopa tapadulcea* Adamski. 2, Wing venation. Scale line = 1.0 mm. 3, Male genitalia. Genital capsule is figured above, aedeagus below. Scale line = 0.5 mm.

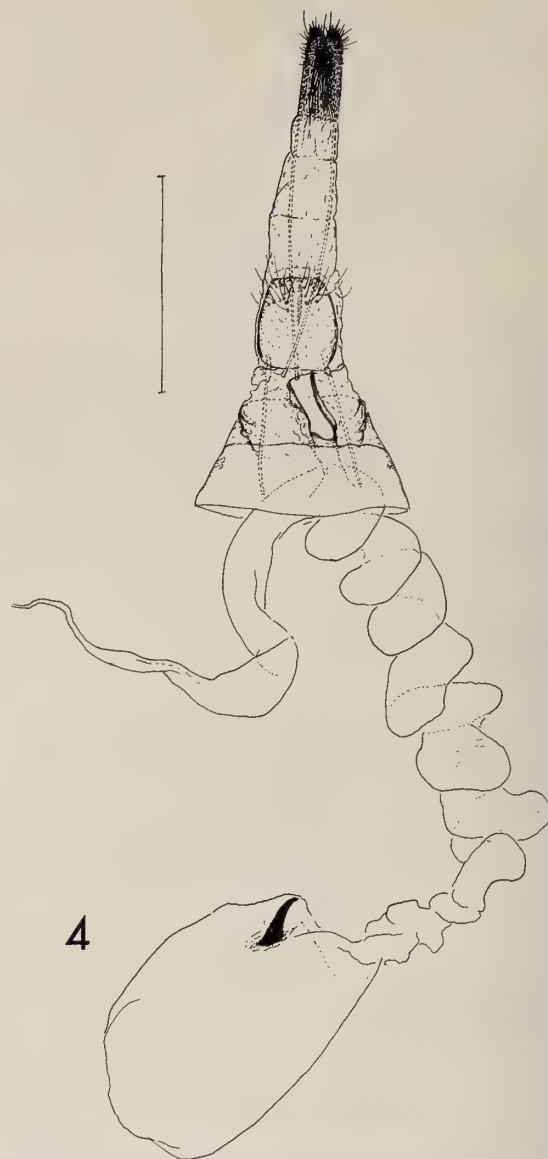


FIG. 4. Female genitalia of *Hypatopa tapadulcea* Adamski. Scale line = 1.0 mm.

near posterior margin of seventh sternum; antrum membranous, short, forming a common inception with ductus seminalis and ductus bursae; basal part of ductus seminalis as wide as posterior part of ductus bursae; ductus bursae spiralled from anterior end of antrum to corpus bursae; corpus bursae with a long hornlike signum.

**Types.** *Holotype*: ♂, "Est[acion] Pitilla, 700 m[eters], 9 k[ilo]m[eters] S[outh] Sta[cion] Cecilia, P.N. Guanacaste, Prov[incia] Guan[acaste], COSTA RICA, C. Moraga, Se[p]t[iembre] 1991, L-N-330200, 380200", "COSTA RICA, INBio, CR1000, 460377" [Bar code label]. Holotype is not dissected and is deposited in

the Entomology Museum at Instituto Nacional de Biodiversidad, Santo Domingo, Heredia, Costa Rica.

**Paratypes:** 75 paratypes: 12 ♂♂, 21 ♀♀, "Est Cacao, 1000–1400 m, Lado SO Vol Cacao, P.N.G. Prov Guan, COSTA RICA, C. Chaves, Abr 1991, L-N-323300, 375700", two dissected males with the following label data, "INBio, Genitalia Slide by D. Adamski, No. 97, Sex ♂", "INBio, Genitalia Slide by D. Adamski, No. 98, Sex ♂", four dissected females with the following label data, "INBio, Genitalia Slide by D. Adamski, No. 99, Sex ♀", "INBio, Genitalia Slide by D. Adamski, No. 134, Sex ♀", "INBio, Genitalia Slide by D. Adamski, No. 135, Sex ♀", "INBio, Wing Slide by D. Adamski, No. 136, Sex ♀"; 3 ♂♂, 9 ♀♀, same label data as above except, "Set"; 6 ♀♀, same label data as above except, "25 Set–11 Oct 1990"; 2 ♀♀, same data as above except, "11 Set–11 Oct 1991"; 1 ♂, 2 ♀♀, same data as above except, "23 Oct–9 Nov 1990"; 1 ♂, same label data as above except, "Mar 1991"; "Est Pitilla, 700 m, 9 km S Sta Cecilia, P.N. Guanacaste, Prov Guanacaste, COSTA RICA, C. Moraga, Set 1991, L-N-330200, 380200", "INBio, Wing Slide by D. Adamski, No. 137, Sex ♀", 5 ♀♀, same label data as above except, "Abr 1991"; 2 ♀♀, same label data as above except, "Set 1991", one female dissected, and with the following label data, "INBio, Genitalia Slide by D. Adamski, No. 100, Sex ♀"; 3 ♀♀, same label data as above except, "2–19 Mar 1992", two specimens collected by P. Rios; "2 ♀♀, same data as above except, "31-Mar–15 Abr 1992, P. Rios"; 1 ♂, same data as above except, "23 Oct–12 Nov 1992, C. Cano"; 1 ♂, 4 ♀♀, "San Luis, Monteverde, Prov Punta, COSTA RICA, 1000–1350 m, Abr 1994, Z. Fuentes, L-N-449250-250850, #2845". Two paratypes deposited in The Natural History Museum, London, England; ten paratypes in The National Museum of Natural History, Smithsonian Institution, Washington, D.C.; all other paratypes in Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica.

**Remarks.** *Hypatopa tapadulcea* is probably more closely related to *H. interpunctella* (Dietz) of Utah, than other known species in the genus. This is based primarily on the similarity of the male genitalia because the female genitalia are structurally very different and do not support close kinship between the two species. Male *tapadulcea* and *interpunctella* share a similarly shaped uncus and gnathos, however, in *interpunctella*, the gnathos is notched. Both have the sacculus longer than wide; in *H. tapadulcea* the distal

margin is obtuse while in *H. interpunctella* the outer margin is subtriangular.

*Hypatopa tapadulcea* ranges from the high altitudes of the northwestern provinces along the Cordillera de Guanacaste southeast to the Cordillera de Tilarán in the Province of Puntarenas. The host for *H. tapadulcea* is unknown.

**Etymology.** The species epithet is derived from a brownish (similar in color to *H. tapadulcea*) crystalline, confectionary cake, *tapa dulce*, that is sold in market places throughout Costa Rica. This sweet is made from sugar cane and is broken into pieces and eaten like candy, or it is mixed with hot or cold water to make *agua dulce*. The *costarriqueños* consider *agua dulce* a national beverage.

Because I have examined the type specimens of all the New World *Hypatopa*, and hundreds of specimens of New World *Hypatopa* representing at least 100 undescribed species, I am confident that *Hypatopa tapadulcea* is the closest known relative of *H. interpunctella*. Many, if not most, undescribed species of Blastobasinae from the New World belong to *Hypatopa*, and with the large amount of museum specimens yet to be examined, the goal of hypothesizing nearest kin and phylogenetic relationships among all these taxa becomes problematic without a comprehensive alpha-taxonomic study.

#### ACKNOWLEDGMENTS

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## POPULATION DEMOGRAPHICS AND THE CONSERVATION STATUS OF THE UNCOMPAHGRE FRITILLARY *BOLORIA ACROCNEMA* (NYMPHALIDAE)

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**ABSTRACT.** *Boloria acrocneuma* is an endangered relict arctic butterfly restricted to fewer than ten colony sites in southwestern Colorado, USA. Pollard transects were conducted from 1990–94 to establish relative population estimates for the butterfly. Results indicate a period of stability and increase for all three colony sites surveyed, and are a contrast to population estimates recorded in the 1980's. Collecting pressure, livestock grazing and local climate change are discussed as potential factors behind the butterfly's original decline and its more recent stabilization and increase.

**Additional key words:** alpine habitat, climate change, collecting activity, Pollard transect, Salicaceae.

*Boloria acrocneuma* Gall & Sperling (Nymphalidae) was discovered on Mt. Uncompahgre in the San Juan Mountains, Hinsdale County, Colorado, and subsequently described by Gall and Sperling (1980) as a new species. The taxonomic relationship of *Boloria acrocneuma* to *Boloria improba* (Butler) has been reviewed (Gall & Sperling 1980, Britten & Brussard 1992) and some authorities recognize *B. acrocneuma* as a valid species (Ferris 1981, Pyle 1981), whereas others consider it a subspecies of the more northern *B. improba* (Scott 1986).

Since 1978, when *B. acrocneuma* was discovered, its demography (Brussard & Britten 1989, Seidl 1995, Ellingson et al. 1996, Wasinger et al. 1997), genetic variation (Britten 1991, Britten & Brussard 1992), and adult and larval life history have been studied (Gall & Sperling 1980, Scott 1982, Gall 1984a, Britten & Riley 1994, Seidl 1995, 1996). Researchers found the species to be in decline in the early 1980's and it was listed as Federally endangered in June 1991 (Opler 1990). Hypotheses for the butterfly's decline include: extensive adult collecting pressure, disruption of larval microhabitat by livestock grazing, and prolonged local drought conditions (Gall 1984a, 1984b, Brussard & Britten 1989, Britten 1991, Britten et al. 1994, Seidl & Opler 1994). The intent of this paper is to summarize and extend data on population size in three populations of *B. acrocneuma* located in the San Juan Mountains in southwest Colorado. Based on these data, I also evaluate the conservation status of the butterfly.

### MATERIALS AND METHODS

**Study Organism.** Like some other alpine butterflies, *Boloria acrocneuma* is thought to have a biennial life cycle (but see Seidl 1996): each cohort overwinters twice and development occurs over three summers, thus creating odd- and even-year broods (Scott 1982, Brussard & Britten 1989). Eggs oviposited the first summer develop into first instar larvae that same sum-

mer and overwinter. The following summer, development through third instar occurs. The third summer, larvae develop through fifth instar, pupate and eclose as adults, which live for approximately seven to nine days (Scott 1982). Britten and Brussard (1992) found no significant genetic differences between the two broods at two colony sites. Population estimates have therefore been characterized as either odd- or even-year broods (Gall 1984a, Brussard & Britten 1989).

*Boloria acrocneuma* specializes on snow willow, *Salix reticulata* L. ssp. *nivalis* (Hooker) Löve et al. (Salicaceae), a common plant restricted to mesic alpine areas in Colorado (Weber 1987). Females exhibit oviposition preference for snow willow (Seidl 1996) and larvae followed in the field feed exclusively on it (Seidl 1995). However, in captivity *B. acrocneuma* larvae will feed on *Salix arctica* (Scott 1982), a close relative to *S. reticulata nivalis*, despite no evidence of the use of this plant having been documented in the field.

**Study Sites.** I conducted population demographic research from 1990–94 at three *B. acrocneuma* colony sites: (1) a colony at Mt. Uncompahgre, the type locality (UP1); (2) a colony within four km of the type locality (UP6); and (3) a colony on Redcloud Peak, ca. 20 km southeast of the type locality (RC1). All colonies are found in glacial cirques with a northeast exposure and range in altitude from 3800–4093 m, with UP1 being the highest in elevation and UP6 the lowest. Each colony site is located in alpine tundra habitat and each contains abundant patches of the butterfly's willow host, *S. reticulata nivalis*. The area encompassed by each of the sites differs—RC1 is ca. 15 ha, UP1 is ca. 20 ha, and UP6 is less than 5 ha. All three study sites occur within public lands: UP6 and UP1 are located in the Big Blue Wilderness Area of the Uncompahgre National Forest, and RC1 is within Bureau of Land Management lands. Hiking trails to both peaks pass through *B. acrocneuma* habitat.

**Population Abundance.** The Pollard transect technique, a simple-to-use, non-intrusive method which identifies trends in butterfly abundance (Pollard 1977,

TABLE 1. Relative population estimates and indexes of abundance for populations of *Boloria acrocynema* 1978–1996, Hinsdale County, Colorado. Prior to 1988, capture-mark-recapture methods were used to estimate population size. Beginning in 1988, Pollard transect methods were used to derive an index of abundance from which a relative population estimate was determined.

Year	Colony <sup>1</sup>			Source
	RC1	UP1	UP6	
1978	NA	NA	NA	Gall 1984a
1979	NA	600 <sup>3</sup>	NA	Gall and Sperling 1980
1980	NA	700	NA	Gall 1984a
1982	1000	500	NA	U.S. Forest Service Files
1987	250–300	4	3	Brussard and Britten 1989
1988	492	200	2	Brussard and Britten 1989
1990	768	NA	NA	this paper
1991	1624	0	20	this paper
1992	948	878	414	this paper
1993	2408	452	2266	this paper
1994	3464	2918	442	this paper
1995	11773	6682	1979	Ellingson et al. 1995
1996	3670	2163	130–200	Wasinger et al. 1997

<sup>1</sup> 1990–1993 estimates were originally derived without intercalculating missing days during the flight season (Seidl & Opler 1994). The data reported here have been reanalyzed such that missing days are calculated as the average of the previous day and the two following days (Cook et al. 1967, Watt et al. 1977).

<sup>2</sup> Gall and Sperling (1980) state that several hundred individuals were seen on 30 July, 1978 but a population estimate for the brood was not calculated.

<sup>3</sup> Gall (1984b) estimated 150–180 individuals at peak flight in 1979 at UP1. In 1980 peak flight estimates of 200 individuals were estimated and found to be associated with a final population estimate of ca. 700, i.e., 3.5 days at peak flight. With this in mind, I have tabulated an approximate population estimation for UP1 in 1979 to be ca. 600, i.e., 3.5 days \* 165 individuals.

<sup>4</sup> During the 1990 flight season I visited UP1 twice and UP6 a single time. These visits do not constitute a thorough search and therefore are specified as NA.

Thomas 1983, Pollard & Yates 1993), was adopted in 1987 to assess trends in *B. acrocynema* abundance (Brussard & Britten 1989). This method is employed by the British Butterfly Monitoring Scheme (Pollard & Yates 1993) and enables researchers to assess population abundance with less intrusive sampling. The main criticism of the Pollard monitoring method is that absolute population estimates cannot be derived from the data since only trends in abundance are recorded and not the fate of individuals *per se*, as in capture-mark-recapture methods (CMR). However, over a long-term monitoring period, the Pollard method can be equally as effective in assessing the condition of butterfly populations (Pollard & Yates 1993).

The method includes laying fixed transect lines in a monitoring area that includes both suitable and less suitable butterfly areas (Pollard & Yates 1993). Since I was concerned that fixed transect lines would disturb *B. acrocynema* habitat, I set new transect lines each field season, placing 100 m long transects in areas of high butterfly density. Transects were walked in the morning and only under favorable conditions: low wind, relatively full sun, and no precipitation. If conditions turned unfavorable, counts were halted to allow poor weather to pass. Transects were walked at approximately 10 min per 100 m transect. Individuals were included in the count if they occurred within five meters on either side of the transect line.

Pollard transects were carried out at the RC1 colony site during the field seasons of 1990 through 1994 and

at the UP1 and UP6 colony sites in 1991 through 1994. Searches for *B. acrocynema* were begun each year in mid to late June. Once butterflies were found, transects were laid and counts were begun within three to five days. Three transects were laid each year at UP6, three to four transects were laid at UP1 each year, and five to eight transects were laid at RC1 each year. The number of transects laid at each site and each year varied with the number of high density butterfly areas found. If a day was missed during the flight season, interim day counts were estimated. These values were derived as the average of the preceding day and two days following the missing transect count after Cook et al. (1967) and Watt et al. (1977).

To determine the relationship between Pollard transect indices of abundance and population estimates, and to derive a *relative* population estimate for comparison among years, CMR experiments were conducted simultaneously with Pollard transects in 1987 at RC1 (Brussard & Britten 1989). Pollard transect data were found to account for approximately 10% of the population estimates derived from CMR methods (Brussard & Britten 1989). Based on these calculations, each daily transect count ( $t_i$ ) was multiplied by 10 to derive the *relative* daily estimate ( $N_i$ ) for a colony.

In addition, Gall (1984b) derived a residency rate for *B. acrocynema*. A residency rate ( $r$ ) is defined as the fraction of animals on day  $i$  that remain in the population on day  $i+1$  and calculates the probability that an individual counted on day  $i$  is recounted the following



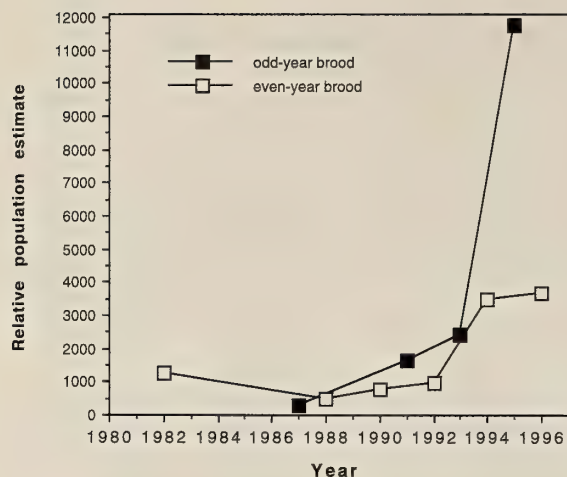


FIG. 1. Relative population estimates for *Boloria acrocnema* at Redcloud Peak, colony site RC1, based on Pollard transect method.

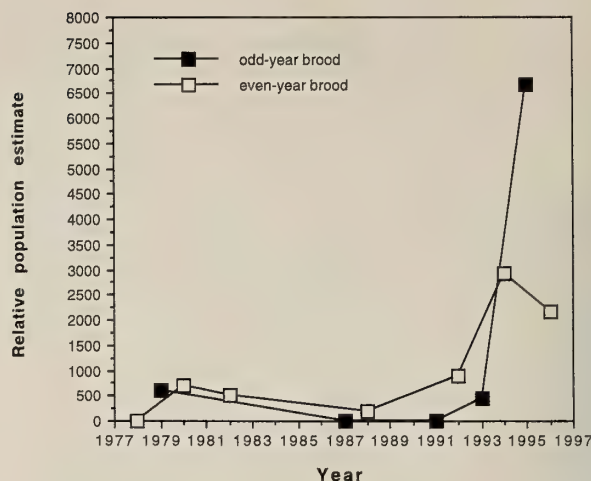


FIG. 2. Relative population estimates for *Boloria acrocnema* at Mt. Uncompahgre, colony site UP1, based on Pollard transect method.

day (Gall 1984b). Residency rates for *B. acrocnema* at UP1 in 1980 were calculated as 0.46–0.70 (Gall 1984b). Therefore, transect counts in this study, and those in Brussard and Britten (1989), were multiplied by the average daily loss rate (1-r) or 0.4.

Total population indices were summed across days to arrive at a relative population estimate for a colony for a given year.

## RESULTS

The even-year population at RC1, initially estimated at maximally 1000 individuals (Gall 1984a), had declined to a count of 492 in 1988 (Brussard & Britten 1989). During this study however, the even-year population increased significantly and relative population estimates for the even-year population include: 768 in 1990, 948 in 1992, and 3464 in 1994 (Table 1, Fig. 1). Similarly, the odd-year population at RC1 increased from 1980's levels; in 1991 and 1993 estimates were 1624 and 2408 respectively (Table 1, Fig. 1).

At UP1, the type locality for *B. acrocnema*, no individuals were seen in 1991, despite a concerted search effort that lasted from July 1 through July 25. However, in 1993 an estimate of 452 was calculated (Table 1, Fig. 2). For the even-year brood, relative population estimates of 878 and 2918 were recorded in 1992 and 1994 respectively (Table 1, Fig. 2).

When the UP6 colony of *B. acrocnema* was discovered in 1988 only two individuals were recorded (Brussard & Britten 1989). An estimate of 20 individuals in 1991 supported the notion that this was a small colony (Table 1, Fig. 3). However, in 1992 and 1994 estimates of 414 and 442 respectively were recorded (Table 1,

Fig. 3). And in 1993 the odd-year brood rose to an estimate of 2266 (Table 1, Fig. 3).

## DISCUSSION

**Population Biology.** Even- and odd-year broods at all three colony sites surveyed in this study have either stabilized or increased when compared to 1980's estimates (Table 1). Original population estimates at RC1 and UP1 were surpassed in 1993 and 1994 and the colony at UP6 grew substantially (Table 1).

In addition to the population data reported here, more current estimates have also been calculated by Colorado Heritage Program researchers using similar methodology (Ellingson et al. 1996, Wasinger et al. 1997). In 1995, the odd-year estimate for RC1 was 11,773, an order of magnitude higher than any odd-year estimate calculated prior to 1995 at that site (Ellingson et al. 1996). Large population estimates were also found at Mt. Uncompahgre colony sites in 1995: 6682 at UP1 and 1799 at UP6 (Ellingson et al. 1996). Although the UP6 estimate is reasonably close to the previous odd-year brood, the estimate at UP1 is more than twelve times as large.

While 1995 estimates were dramatically different from 1993 estimates, 1996 estimates derived by Colorado Heritage Program researchers were more similar to those found in 1994. For instance, the estimate at RC1 in 1996 was 3670 (Wasinger et al. 1997): in 1994 I found 3464 (Table 1). At Mt. Uncompahgre, the estimate at UP1 was 2163 in 1996 (Wasinger et al. 1997) and 2918 in 1994 (Table 1). Finally, the estimate at UP6 was 130–200 individuals in 1996 (Wasinger et al. 1997) and 442 in 1994 (Table 1).

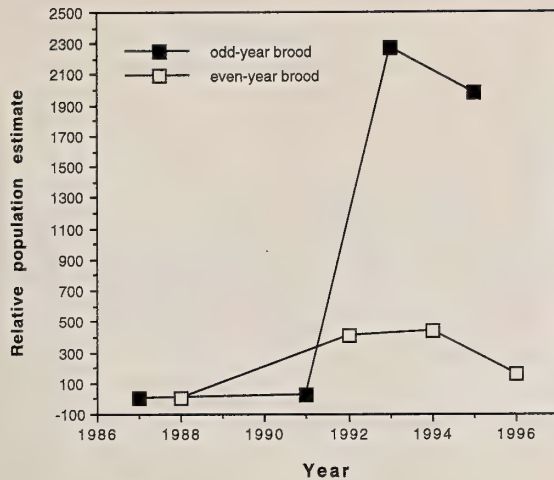


FIG. 3. Relative population estimates for *Boloria acrocynema* at Mt. Uncompahgre, colony site UP6, based on Pollard transect method.

Data from 1990–96 provide strong evidence that *B. acrocynema* is on a trajectory toward stabilization or increase. Yet the following caveats need to be mentioned: 1) employing the CMR calibration calculation of 10% to transect counts may lead to inflated estimates since the CMR results from one colony site may be not transferable to other sites; and 2) residency rates may change between years and are largely determined by the geographical area that the colony inhabits. For instance, the UP6 colony site is one third the size of UP1 and RC1: three transects at UP6 include the majority of available *S. reticulata nivalis* habitat. Therefore, the likelihood of counting individuals on day  $i+1$  that were present on day  $i$  is higher at UP6 than at RC1, due to the differences in area and assuming all else being equal. To remedy these problems in deriving present relative population estimates, CMR experiments and local residency rates should be calculated for all colony sites. Those values should then be used to translate Pollard transect data into population estimates.

**Conservation Status.** Collecting pressure in the early 1980's was reported to be intense and some collectors extracted more than 50 specimens at any given time (P. A. Opler, pers. comm.). Although there are no studies that show collecting to be the cause of local extinction in Lepidoptera (Pyle et al. 1991), studies of vertebrate fauna demonstrate that overharvesting can reduce genetic variability and heterozygosity (Bonnell & Selander 1974, O'Brien et al. 1989, Barrowclough & Gutiérrez 1990). Conservation biologists assume that populations with greater genetic variability are better able to survive and evolve in changing environments (Avise 1994).

Livestock grazing is the second force proposed by some to have affected *B. acrocynema* (Seidl & Opler 1994). Sheep grazing in the alpine environments of the San Juan Mountains began in the mid 1800's (Lake City, Colorado Historical Society) and continues into the present. Foraging and trampling by sheep may result in lower seedling survival of both nectar sources and host plants (Owens & Norton 1992).

Both collecting and livestock grazing have been prohibited or suspended since *B. acrocynema* was federally listed in June 1991, presumably shielding the species from these pressures. However, local climate change and a consequent drying trend have not abated. Weather data collected over the last two decades indicate a trend of below-average snowfall and higher-mean ambient air temperatures for southwestern Colorado (Colorado Avalanche Center, Denver, Colorado).

It has been demonstrated that weather can influence butterfly populations (Pollard 1988, Pollard & Yates 1993) and that catastrophic weather events may bring about local butterfly extinction (Ehrlich et al. 1972, Singer & Thomas 1996). Based on the unusual distribution and microhabitat requirements of *B. acrocynema*, its relict arctic history, specialist nature, and mesic habitat requirements, this species may be an excellent indicator of the effects of climate change in alpine environments. Although some species may migrate to cooler northern latitudes (Parmesan 1996), species with low vagility like *B. acrocynema* may be limited in their dispersal capabilities (Dennis & Shreeve 1991, Murphy & Weiss 1992, Britten et al. 1994). Changes in host plant quality, phenology and distribution are also likely as plants respond to changing abiotic conditions (Dennis & Shreeve 1991). Butterfly abundance may be affected as host plants become less palatable or less available (Dennis & Shreeve 1991, Pollard & Yates 1993).

Britten et al. (1994) suggested that *B. acrocynema*'s low population numbers in the late 1980's were due to human-induced factors including climate change and that the butterfly was headed for extinction. The data I have reported here suggest that the butterfly has recovered from its low population numbers. However, I believe Britten et al. (1994) raised important questions concerning the effects of climate change on *B. acrocynema* and other high altitude mesophilic butterflies. To address their concerns, careful analysis of how climate change parameters (rising ambient temperatures, increased UVB, elevated CO<sub>2</sub> levels, etc.) affect the larvae and adults of *B. acrocynema* (or a close surrogate due to its endangered status) is needed. These experiments will provide essential evidence in identifying current and potential effects of climate change



on *B. acrocne* and will help to predict the species' future population dynamics and its probability of extinction under a climate change model.

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PATTERNS IN THE SPATIAL AND TEMPORAL USE OF TEXAS MILKWEEDS (ASCLEPIADACEAE)  
BY THE MONARCH BUTTERFLY (*DANAUS PLEXIPPUS* L.) DURING FALL, 1996

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**ABSTRACT.** In an attempt to better understand the fall migration of the monarch butterfly (*Danaus plexippus* L.) through Texas, the spatial and temporal distribution of milkweeds and immature monarchs were monitored along an 800 km transect. Important monarch host plants were found to be distributed unequally along the transect. Breeding monarchs were present at least one month before the main body of migrants appeared. The distribution of eggs and larvae did not spatially follow the distribution of milkweeds. Some milkweed species and locations were used more than others. Possible explanations for the distribution patterns observed include the circumscribed nature of the fall migratory pathway and the foraging efficiency of the polygyne version of the imported fire ant.

**Additional key words:** natural regions, oviposition, fire ant, *Solenopsis invicta*, *Asclepias*, migration.

Although the monarch butterfly (*Danaus plexippus* L.) is the best known of North America's migratory insects, much remains to be learned about the spatial and temporal patterns of how it populates and then vacates northern North America each spring and fall (Brower 1995). Our basic understanding of this process is as follows: During summer, the eastern group of monarchs spends two or more generations breeding in North America above latitude 35° (Malcolm et al. 1993). In late summer and early fall, the progeny of summer breeders migrate to central Mexico, crossing much of the North American continent (Urquhart 1987). They spend five months at the Mexican overwintering sites, most of the time in a state of reproductive dormancy. After mating in late winter and early spring, they fly northward to once again exploit the milkweed flora (Cockrell et al. 1993) widely distributed throughout North America (Woodson 1954). During spring and summer in their northern breeding grounds, they greatly increase their numbers, reversing the population decline that occurs during fall and winter.

To understand more about monarch population dynamics in Texas and the implications for the monarch population of North America, this study investigated the presence and abundance of monarch immatures on milkweed flora (Asclepiadaceae) in Texas during the fall of 1996.

MATERIALS AND METHODS

Milkweeds were examined along two routes between 30°N and 32°N latitude. One route extended east from Austin to Pineland in Sabine County in extreme eastern Texas near the Louisiana border and the other extended west from Austin to Ozona in Crockett County in West-central Texas (Fig. 1). A loop was made at the eastern end to insure that areas where single-queen (monogyne) fire ant colonies had been reported were well covered (Anonymous 1998; E. Vargo,

pers. comm.). The two segments combined, referred to below as the cross-Texas transect, stretched about 60% of the way across Texas from 31.25°N, 93.985°W at Pineland to 30.00°N, 101.201°W at Ozona, a distance of 801.66 km (ca. 900 road kilometers; see Marvin 1939, Table 92). The transect was traversed three times during the fall migratory season. The east and west segments of the first transect were conducted on 20–23 September and on 27–29 September respectively. The second transect was conducted on 6–7 and 11–13 October and the third on 12–13 and 12–13 November. On the first transect to West Texas (27–29 September), the return route was slightly different from the two subsequent transects. Instead of proceeding directly to Austin along Highway 290, a parallel route 30 km to the south of the regular route was taken. This route followed Interstate 10 to Comfort and then proceeded eastward along Highways 473, 281 and 165, rejoining Highway 290 at Henly. The last transect to East Texas (12–13 November) ended at Madisonville. The transect was truncated here because no activity had been observed on the previous transect (6–7 October), and none had been observed prior to Madisonville.

The scheduling of the transects was based on Texas Monarch Watch reports of the presence of monarchs in the state. Transect dates were chosen to cover periods before the main body of migrants arrived, during the peak of the migration and after most monarchs had cleared the state. (The Texas Monarch Watch is an educational outreach service that solicits reports from volunteers concerning the presence and abundance of monarchs in the state (Calvert 1993–1997, Calvert & Wagner in press).)

The relative abundance of milkweeds was assessed along the cross-Texas transect by counting stems whenever milkweeds were sighted. During September and October, many milkweeds were in flower and their presence was very conspicuous. Sampling stops were



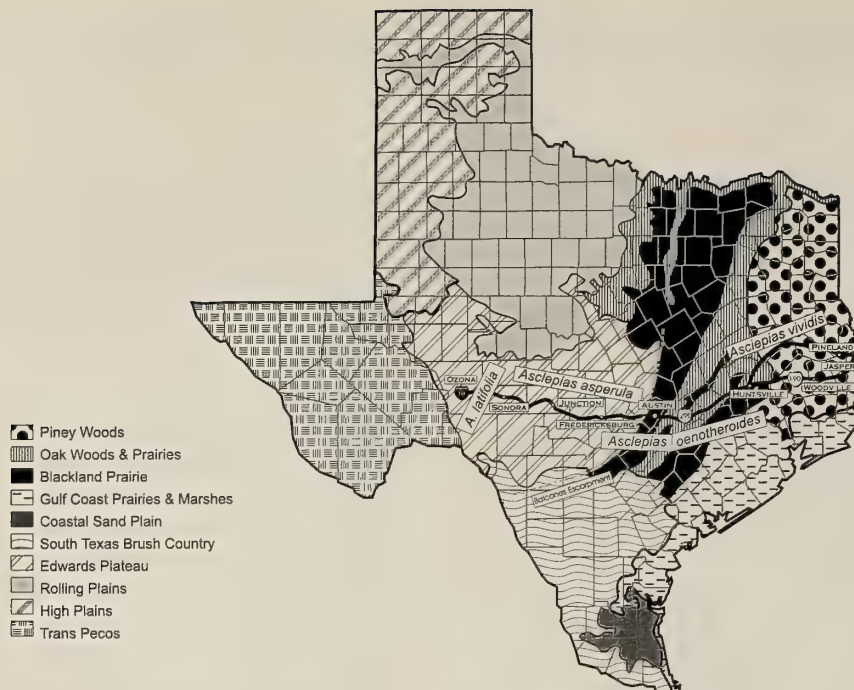


FIG. 1. The cross-Texas transect route showing the location of milkweeds important to monarch butterflies along the 800 km transect from Pineland to Ozona.

made when milkweeds were spotted in adjacent fields or roadside right-of-ways. Areas that appeared to be prime milkweed habitat such as short grass prairies and areas with poor soils were also searched. During November, when many fewer milkweeds were in flower, plants were located by revisiting areas where they were found abundant on previous transects.

This study focused on the four abundant *Asclepias* species found in central Texas: *Asclepias viridis* Walt., *A. oenotheroides* Cham. & Schlecht, *A. asperula* Wood, and *A. latifolia* Raf. Other rarer species were examined as encountered, e.g., *A. texana* Heller and *A. curassavica* L. Milkweed vines in the genera *Matelea*, *Sarcostemma* and *Cynanchum* were also sampled, but only sporadically. Due to the very different growth form of these species and the difficulty of following a stem through the tangle of vines, the effort of examination cannot be considered the same as for the other species.

Although every effort was made to keep the search method constant, initial search times were longer than later ones. It took less time to relocate milkweed patches after their initial discovery. Nonetheless, since the search method was always the same, the number of milkweeds counted should serve as a rough index of relative abundance of each host species in the genus *Asclepias* through space and time.

During a sampling stop, the identity of the milkweed species was verified, the stem lengths were measured, and the number of eggs and monarch larvae on the stems were counted. When available, 20 or more stems were examined. If fewer than 20 stems were present, all available stems were measured and examined. Time of day, location, and the presence of adult monarchs were also noted. Geographical locations of sampling sites were determined from a U.S. Geological Survey Map of Texas (Anonymous 1985).

A problem arose concerning the identification of eggs. At some locations in West Texas, both queen (*Danaus gilippus* L.) and monarch larvae were present at the same time during the fall. Since monarch eggs cannot be distinguished from queen eggs, eggs from both species were counted and are included in the totals. Excluding the larvae present on *M. reticulata*, the host species that was used only by queens, 36% of the larvae encountered in West Texas were queens. No queen adult or larvae were encountered along the eastern segment of the transect. All eggs here were considered to be monarch.

## RESULTS

**Relative abundance and distribution of milkweed species used by monarchs.** Approximately

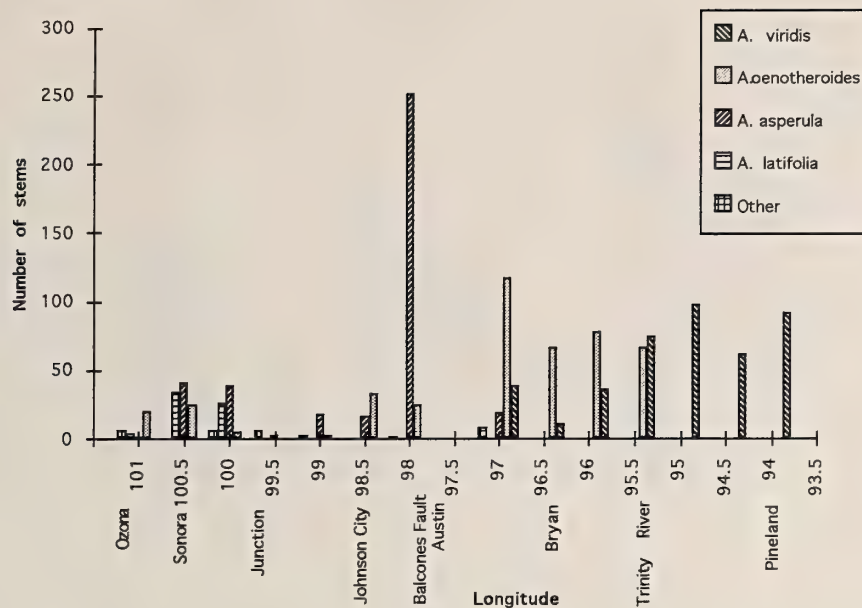


FIG. 2. The relationship between longitude and the occurrence and relative abundance of the principal monarch host plants.

midway between Ozona to Pineland, the 800 mile transect crossed a major biogeographical barrier—the Balcones Fault (Fig. 1). At the latitude of the transect, the Balcones Fault is located at Austin (97.67°W). The transect west of the Balcones Fault lies entirely within the Edwards Plateau. Elevations here are 250–300 meters higher than the transect area to the east of the fault. East of this line rainfall is ample, >32 inches per year; west of it rainfall diminishes to ca. 16 inches per year at Ozona (101.2°W longitude; Arbingast, et al., 1973). Proceeding from east to west, the transect crossed four natural regions: Piney Woods, Oak Woods and Prairies, Blackland Prairie and Edwards Plateau (Anonymous 1978). The diminishing rainfall as one proceeds westward is conspicuous in the change in natural regions, the reduced density and stature of the trees, and the change in distribution of milkweeds.

Above average rainfall during the fall of 1996 (Anonymous 1997) produced luxuriant crops of milkweed giving ample opportunity to observe their distribution and relative abundance (Figs. 1, 2). In October, when the four major hosts (*A. viridis*, *A. oenotheroides*, *A. asperula* and *A. latifolia*) were at their peak of flowering, *A. viridis* accounted for 41% of the milkweeds along the transect followed by *A. asperula* (33%), *A. oenotheroides* (17%) and *A. latifolia* (4%).

The distribution of these species along the transect varied with longitude. *Asclepias oenotheroides* had the widest longitudinal range (Figs. 1, 2). It was distrib-

uted in patches throughout most of the transect, but was not found east of the Trinity River. It appears to be mainly a prairie species, reaching its highest density in the regions between Austin (97.67°W) and Midway (95.75°W). However, it was also consistently, but rarely, encountered in the Edwards Plateau to the west end of the transect at Ozona.

*Asclepias asperula* was the dominant milkweed in the genus *Asclepias* on the Edwards Plateau (Figs. 1, 2). It was mainly present in patches of multiple-stemmed rosettes along roadsides and in pastures. It was found as far east as longitude 97.45°W in the Oak Woods and Prairies region between Bastrop and Austin, but east of Austin, it was rare. The highest densities were found between Austin and Johnson City. *A. latifolia* was encountered only in rare patches on the Edwards Plateau west of 100°W longitude.

The Balcones Fault at Austin divides the ranges of *A. viridis* and *A. asperula* fairly well (Figs. 1, 2). Proceeding eastward from Austin, *A. viridis* began a more or less continuous distribution around 97°W and, with two gaps, continued into the East Texas Piney Woods to the end of the transect at Pineland (93.99°W; Fig. 2). East of Austin, *A. viridis* reaches its greatest abundance in a zone extending along Highway 21 approximately 65 km on either side of the Trinity River (95.70°W longitude). This area corresponds to an area of warmer than expected temperature that extends northward along the Trinity River (Fig. 1; Arbingast, et



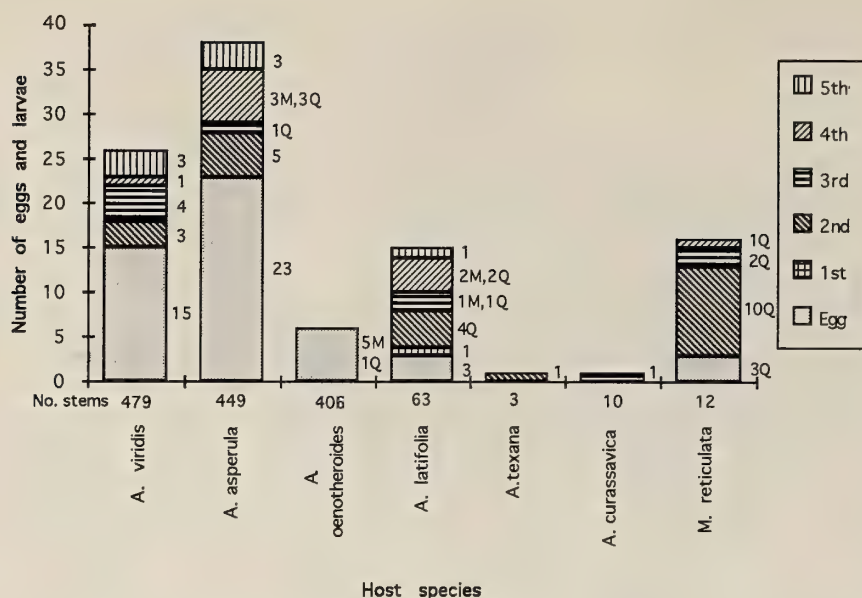


FIG. 3. Numbers of eggs and larval instars found on various milkweed hosts along the cross-Texas transect during the fall of 1996. M = monarchs (*Danaus plexippus*); Q = queen (*Dannaus gilippus*). Numbers not followed by a letter are monarchs.

al. 1973). Within this area the number of days of frost free weather are ca. 35% greater than regions above the Balcones Fault on the Edwards Plateau. The presence of dense stands of *A. viridis* corresponded well with the occurrence of Blackland Prairie and with pockets of prairies within the Oak Woods and Prairies Natural Region. Although dense stands occurred in some places within the Piney Woods, *A. viridis* in this area was confined to roadsides. Because of this restriction, its overall abundance here must be considerably less than in the prairies.

Two other milkweeds in the genus *Asclepias* were encountered along the transects. One stem of the non-native *A. curassavica* was found in a garden in Johnson City, and three stems of *A. texana* were found along Highway I 10 at ca. 99.0°W.

Several milkweed vines were encountered in the western portion of the transects. These included *Cynanchum barbigerum* Shinnery, *Sarcostemma crispum* Benth., *S. cynanchoides* Dcne., and *Matelea reticulata* Woods. Both *M. reticulata* and *S. cynanchoides* achieve high biomass in the western portions of the transect.

Stem counts of the four major milkweed species during the three months indicated that all species of milkweeds except *A. oenotheroides* declined in abundance from October to November. Only *A. oenotheroides* became more abundant at the end of the three month period. The continued growth of *A. oenotheroides* may be explained by the apparently positive response of

this species to the mowing of highway right-of-ways by the Texas Department of Transportation (Calvert, unpubl. obs.).

**Distribution of monarch eggs and larvae with respect to host species, location and time in the season.** Prior reports to the Texas Monarch Watch indicated that in previous years, breeding monarchs had been present in low densities in Central Texas during September, and that the main mass of migrants did not arrive until the end of September. Migrants had mostly cleared the north and central parts of the state by the end of October (Calvert 1993–1997, Calvert & Wagner in press). Cross-Texas transects commenced on 21 September and continued until 18 November.

A total of 1422 milkweed stems were measured and examined for the presence of monarch and queen eggs and monarch larvae. Eggs and larvae per meter of stem were not equally distributed among milkweed species (Fig. 3). *A. texana*, *A. curassavica* and *M. reticulata* were infrequently encountered on the transects, but each of these species had eggs or larvae. Of the four major milkweed species encountered, leaves of *Asclepias latifolia* had the most eggs and monarch and queen larvae per meter of stem (0.73 eggs and larvae/m) and *A. oenotheroides* had the least (0.09 eggs and larvae/m). *Asclepias asperula* and *A. viridis* had 0.27 and 0.39 eggs and larvae/m respectively. Monarchs and queens used *A. latifolia* much more than any other milkweed species—almost three times more than *A. viridis* and ca. two times more than *A. asperula*.

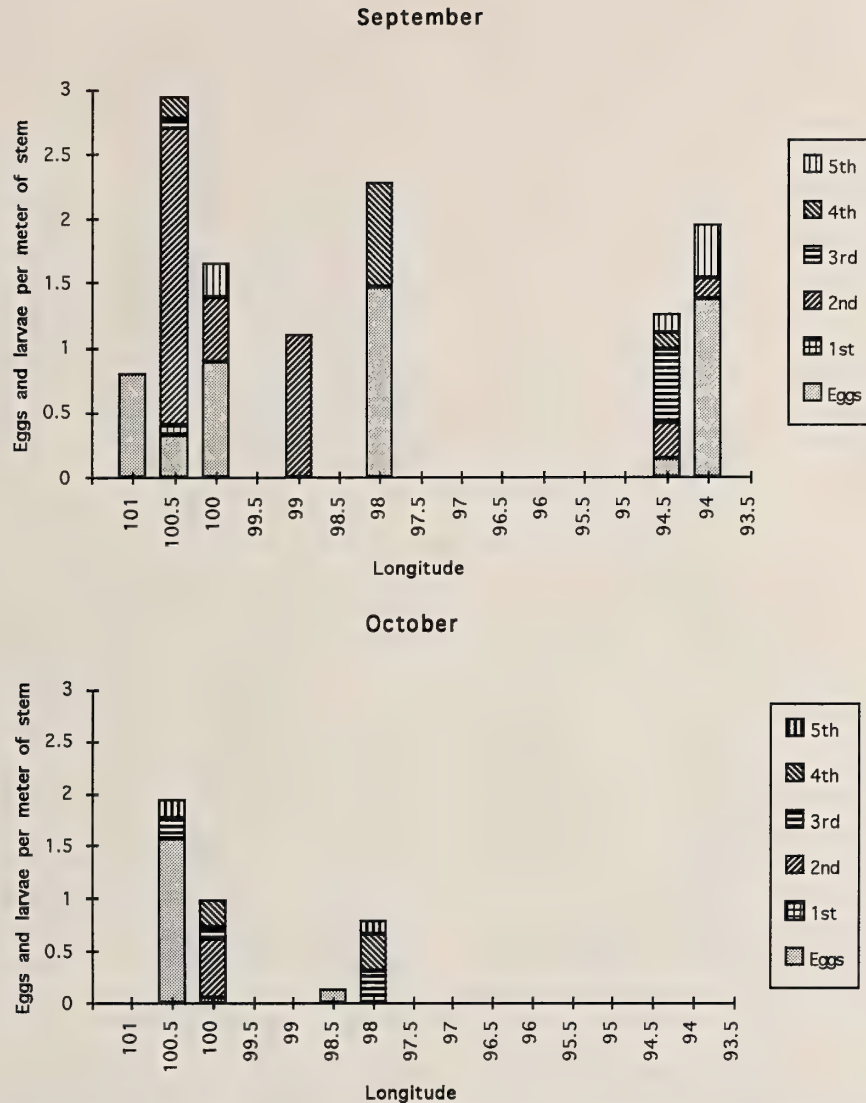


FIG. 4. The relationship between numbers of eggs and larvae per meter of stem and the time of the transect. Breeding activity declined from a high in September to near zero in November. **a**, September; **b**, October;

Most of the milkweed patches encountered were comprised of one plant species. Only rarely were two species found in the same area, e.g., *A. oenotheroides* and *A. viridis* in East-central Texas and *A. latifolia* and *A. asperula* in West Texas. Because of the spatial separation of host species, these data do not show oviposition preferences among the hosts, but rather, they show a presence in a specific geographic area.

Cursory searches of vines in the genera *Cynanchum* and *Sarcostemma* revealed no eggs or larvae. Although it has been reported that *Matelea* is not used by monarchs (P. Davis, pers. comm.), the importance of these other potential milkweed vine hosts needs to be investigated.

During the fall of 1996, the presence of eggs and larvae at both ends of the transect declined as the season advanced. Eggs and larvae were encountered on milkweeds east of Austin (97.67°W) during the initial transect of 20–23 September, but not on the two subsequent transects of 6–7 October and 12–13 November (Fig. 4a–c). In contrast, monarch and queen eggs or larvae were observed west of Austin during each of the three transects run from 27 September to 17 November (Fig. 4a–c); however, the last transect of 17–18 November yielded no eggs and only one larva. The total number of eggs and larvae for the complete transect declined from a September high of 69, to 26 in October, to 1 in November. Breeding in East Texas



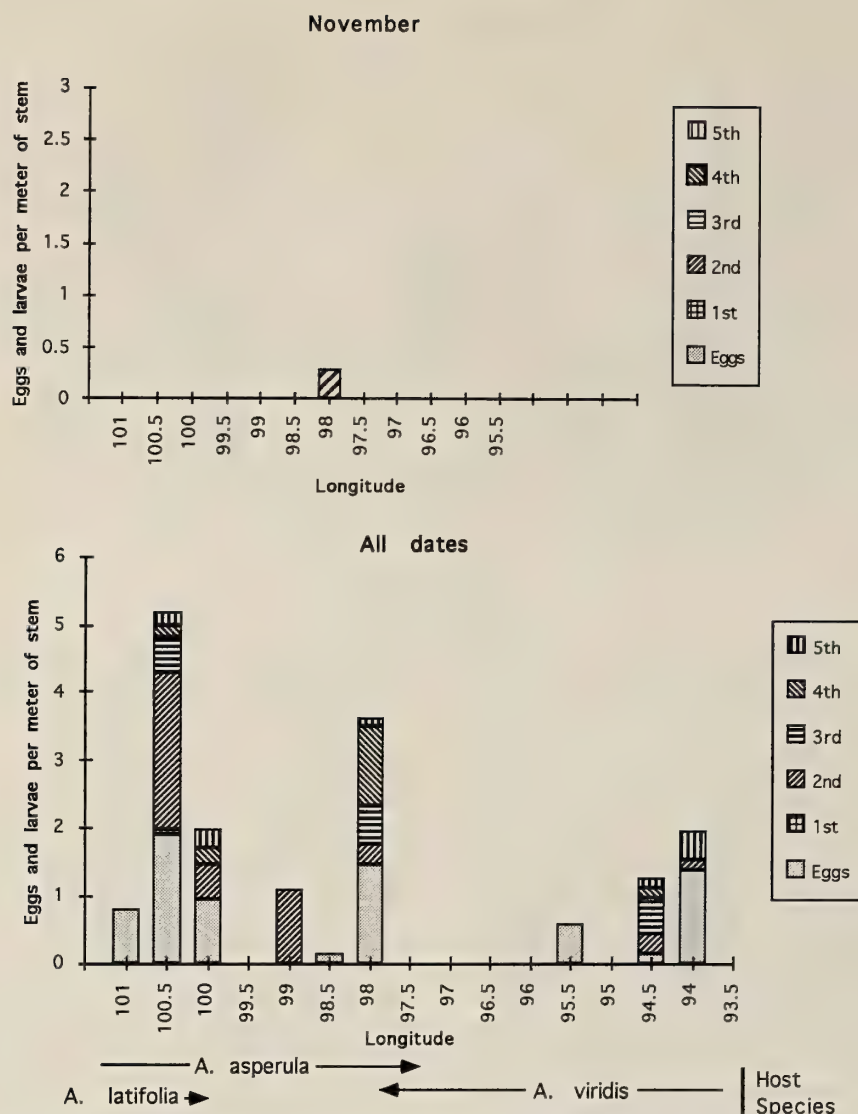


FIG. 4. c, November; d, all dates combined. A conspicuous gap in breeding activity occurs in the central prairie area between and including 96°W and 97.5°W in spite of the presence of milkweed there.

was likely over by the time the main mass of migrants arrived, but continued into November in West Texas (see discussion below).

Monarch (and queen) eggs and larvae showed a bimodal distribution along the 800 km transect (Fig 4d). The most eggs and larvae per meter of stem were found west of Austin between longitudes 98° and 101°W. The main concentration on the western end began about 15 miles east of Sonora (100.78°W) and continued to Ozona (100.96°W). Another area of concentration was south of Johnson City (98.37°W). Conspicuously and curiously absent were monarch eggs and larvae located in the center of the transect, from Austin (97.87°W) to Huntsville (95.55°W), the main

prairie region of these latitudes in Texas. Traveling eastward, the number of eggs and larvae increased east of Livingston (94.63°W) and were especially concentrated in patches in the Piney Woods between Broadus and Pineland (94.14°W). Averages for the fall of 1996 were 0.16 eggs and larvae/meter of plant stem east of Austin ( $n = 820$  stems) and 0.47/meter of plant stem ( $n = 602$ ) stems west of Austin. Most of the fall breeding activity occurred west of Austin, and most of it occurred on *A. latifolia*.

#### DISCUSSION

**The distribution of milkweeds and monarch eggs and larvae with respect to the distribution of**

**milkweeds.** With the exception of one major gap between Broadus and Crockett and several minor gaps elsewhere (Fig. 2), milkweed species were continuously distributed throughout the transect. Monarch and queen eggs and larvae were not. The concentration of eggs and larvae in the eastern and western end of the transect and their absence in the middle prairies, in spite of the presence of milkweeds, requires explanation. Two possibilities are: 1) Monarchs migrating south during the fall largely avoid the east-central prairies, and therefore little oviposition occurs there. 2) The predacious activity of the imported fire ant, *Solenopsis invicta* Buren primarily determines the distribution of eggs and larvae. The first hypothesis corresponds well with data compiled from the Texas Monarch Watch. The fall migratory flyway is mainly located to the west of Austin and corresponds to the western end of the transect (Calvert & Wagner 1999). However, the migration did not reach Texas until after breeding had ceased in East Texas. Moreover, monarch eggs and larvae had already appeared in West Texas before the beginning of the migration.

The second hypothesis best explains the bimodal distribution of monarch eggs and immatures during the fall of 1996. The absence or low densities of fire ants in West Texas may explain the relative abundance of eggs and larvae in that region, while the preponderance of the far less dense single-queened colonies in East Texas (Porter et al. 1991) may allow a relatively higher number of eggs and larvae to survive there.

Other studies support the contention that fire ants are important in the decline of many species of Lepidoptera in Texas. Long term records of the presence and abundance of Lepidoptera show that the abundance of lepidopterans in the vicinity of Austin has fallen to 50% of pre-fire ant levels. Especially hard hit were grass-feeding members of the Satyridae (C. Durdin, pers. comm.). During the spring of 1995, a field in South central Texas near Luling containing an estimated 1250 monarch eggs failed to yield a single late instar monarch larva (Calvert 1996). This same field contained an estimated 1001 fire ant mounds. The high mound density and renowned foraging efficiency of the imported fire ant (Porter et al. 1991) suggested that this predator was the principal culprit in decimating the monarch population. Finally, preliminary results from a study comparing larval growth inside exclusion zones, where fire ants densities were kept relatively low, to areas outside the exclusion zones, showed the production of fifth instars inside the exclusion zones to be 13 times higher than outside. (Calvert, unpubl. data).

The distribution of prairies in the mid-west and the pattern of the spring migration northward through

Texas suggests that the monarchs that breed on Central Texas prairies and plains are the progenitors of monarchs that will breed on the prairies of mid-western states further north (Malcolm et al. 1993). The pattern of ample oviposition, combined with the failure of larvae to develop into later instars, found during the spring of 1995 near Luling (Calvert 1996), suggests that monarchs breeding within the fire ant zones of Texas make only a small contribution to the North American monarch population. No evidence yet exists for similar effects in areas farther east where fire ants are also abundant, but eastern fire ants colonies are mostly monogyne and are not as dense as the multiply-queened (polygyne) variety on Texas prairies (Porter et al. 1991). The reproductive success of monarch migrants passing through in the fall may be diminished for the same reasons.

**Fall breeding in Texas.** It has long been held that monarchs greatly increase their population size during summer months by breeding in the northern portion of their North American domain, especially in the latitudes of the Great Lakes and Northeastern States (Urquhart 1987; Malcolm et al. 1987). This is the area where the greatest biomass of one of their important milkweed hosts (*A. syriaca* L.) is found. At the peak of breeding (June and July), all females contain ovaries with numerous eggs in the oviducts and there is no communal roosting. During this period there are virtually no monarchs in Texas (Calvert 1993–1997). As the season advances into September, more and more females possess inactive ovaries and communal roosting increases. At the beginning of their southward migration, most individuals show inactive ovaries and testes, but occasionally males and females with active reproductive organs are encountered (Brower 1985). It was recognized that some breeding did occur on the way south in states such as Texas, but the extent and importance of this was not known (Urquhart 1987).

These data show that most fall breeding occurred early in the cycle before the main mass of migrants had arrived. Only in West Texas was there any breeding activity after the beginning of October (Fig. 4b). Prior to the arrival of the great masses of migrants, only an occasional monarch has been seen in Texas (Calvert 1993–1997), and communal roosting has not been observed. The early population, which may arrive as early as late August, may differ from the main migrant body in its breeding activity and non-communal roosting. It may not be part of the migratory movement to Mexico. Instead these may be breeding butterflies that have dispersed southward in the same manner that they disperse northward in the spring, stopping to lay eggs as the opportunity presents itself.



The presence of breeding monarchs in Texas in late August and early September was unexpected and requires a rethinking of the pattern of migration. Future studies may show that monarchs regularly breed on Texas milkweeds during September and perhaps October, augmenting their numbers and adding a generation to the monarch life history cycle. The origin of these late summer breeders is of yet undetermined.

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## BOOK REVIEWS

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DIE NOCTUIDEN RUMANIENS, by L. Rakosy. 1996. Published by Staphia 46. 648 pp., 30 color plates, 11 habitat photographs, 68 text figures, 821 line drawings of genitalia, 651 distribution maps. Hard-back, 28/21 cm. Available from Apollo Books Aps., Kirkeby Sand 19, DK-5771, Stenstrup, Denmark, Tel. 45-62-26-3737, FAX: 45-62-26-3780. Price DK 560.00 (approximately U.S. \$90.00).

Here is a remarkably fine work focusing on the rich noctuid fauna of a large eastern European area between the Carpathian Mountains, the lower Danube with its delta, and the Black Sea. The author, who is one of Romania's leading experts on the Noctuidae, has done many years of research in the field and museum collections. This book is the pinnacle of all those years of work.

It starts with an introductory section, written in cooperation with Dr. Eckbert Schneider, which presents a history of noctuid studies performed in the territory of present-day Romania since as early as the 18<sup>th</sup> century. In the following sections, Romania's geography and landscape are presented and the country's climate and vegetation are discussed. Several beautiful, colored illustrations complement the text, showing images of various biotopes from the high peaks of the Carpathian Mountains to the sand dunes on the Black Sea coast.

Next, a brief section discusses the biogeography of the Romanian noctuid fauna. It has been discovered, among other things, that about 5% of Romania's noctuids are holarctic in distribution, and so Romania shares over 30 noctuid species with North America (e.g., *Scoliopteryx libatrix* (L., 1758); *Acronicta auricoma* (F., 1787); *Plusia putnami* Grt., 1873; *Calophasia lunula* (Hufn., 1766); *Xanthia togata* (Esp., 1788); *Agroperina lateritia* (Hufn., 1766); *Hydraecia micacea* (Esp., 1789); *Cerapteryx graminis* (L., 1758); the recently introduced *Noctua pronuba* (L., 1758)). The anatomy of the imago, egg, larva, and pupa is described in a concise and clear manner with very good illustrations. The author highlights the important features of the adult exoskeleton, genitalic structures, egg morphology, and larval chaetotaxy.

The systematic part forms the bulk of the work. Each of the 670 species ever to be recorded on Romanian territory is discussed in detail. The author follows the systematic list of the European Noctuidae published by Fibiger and Hacker (1991). He gives a brief structural and genitalic description for each genus and treats each species by giving a list of selected synonyms with authors and years, biological data for the adult and the larva, general distribution and distribution within Romania. For many species there are very interesting parasitologic mentions. It is worth mentioning here that the author is describing two new subgenera (*Synapamea* for *Apamea Ochsenheimer*, 1816 and *Denticucullus* for *Chortodes* Tutt, 1897) and seven new subspecies of local/regional importance from endemisms in Carpathian Mountains.

The illustrations of the male genitalia for each species and the female genitalia for many species are grouped together after the systematic section. The author has made a tremendous effort in personally drawing a total of 821 excellent illustrations of these important diagnostic tools. The distribution within the country is illustrated with the record/dot system and there is a map for each species with valid Romanian records.

Bound together at the end of the text are 30 colored plates that show 882 excellent quality photographs of adults of each species discussed in the work. The impeccable quality of these plates as well as of the photographed specimens make identification by superficial habitus possible even for the most difficult groups (e.g., *Oligia* Hbn., 1821; *Cucullia* Schran, 1802; *Orthosia* Ochs., 1816, etc.). The plates are followed by 3 more beautiful, folding plates that show 40 stunning photographs of live larvae.

This work contains an extensive list of literature with 549 references on Romanian and general European papers and books discussing noctuid related topics. The book ends with an Index that lists all genera, species, and synonyms with their authors and years of description. Unfortunately, the book lacks a species checklist,

making the overall faunistic appreciation of the area and the comparison with other areas somewhat difficult and time consuming.

Because it covers 670 species of Noctuidae from Europe (over 50% of the whole continental fauna), this book is a landmark work. It is the first one to treat exhaustively a moth family (and of the magnitude of the Noctuidae!) in an eastern European country and with color photographs and genitalic illustrations for all listed species. Hacker did something similar when he published his book about the noctuids of Greece (1989, *Die Noctuidae Griechenlands, Mit einer Übersicht über die Fauna des Balkanraumes (Lepidoptera: Noctuidae)*, *Herbipoliana* 2:1–589) but he only illustrated a selected number of adults and not all of them in color, with selective genitalic drawings. These two books, Hacker's and Rakosy's complement each other very well by giving a very good idea of the composition of the noctuid fauna of Eastern Europe from the Mediterranean Sea to the Ukrainian Steppe.

Although written in German, the text can be understood with basic linguistic skills, making it an important source of information on the noctuids in general and a very good identification tool for the over 30 noctuid species shared by Romania and the U.S.A.

Mr. Rakosy and his publisher, the Austrian house Staphia 46, are to be very highly praised for producing a book of the highest informative and graphic standards, making of it a most valuable tool for the serious student of this large and heteromorphous family.

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CONTRIBUTIONS TO THE KNOWLEDGE OF THE INSECTS OF THE PHILIPPINES, III. [Beiträge zur Kenntnis der Insekten der Philippinen, III], edited by Wolfgang A. Nässig, Colin G. Treadaway and Josef Settele. 1998. *Nachrichten des Entomologischen Vereins Apollo* e. V. Frankfurt am Main, Supplement 17, July 1998. Senckenberganlage 25 D-60325 Frankfurt am Main. 576 pp., 48 color plates, text figures. ISSN 0723-9920.

The Philippines is an archipelago of 7107 islands, many are very small in area with only about 500 islands with an area over one Km<sup>2</sup>. Only 2100 islands are actually inhabited by 65 million people composed of 60 ethnic groups. Not surprisingly, about one third of the islands are not listed by name in most reference books or maps. The Philippine Islands, with the highest mountain reaching 2954 m and with 17 active volcanoes, is geologically very complex. The zoogeographical relationships to other areas of southeast Asia are manifold and complicated.

Historically, the Philippines was noted for its extensive forest coverage. However, this has changed considerably over the past 30 years and now less than 10% remains of the original forest coverage present 50 years ago. Although there are 61 national parks and protected areas, there will be no true forests shortly after the turn of the century if the current rate of deforestation continues. This will have a very strong impact on all forms of life in Philippine forests including insects.

Human pressure on the global environment makes it critical that we acquire knowledge about biological diversity as fast as possible. An essential contribution to managing the biosphere intelligently is to discover, describe, and inventory its species. Southeast Asia is by no means an exception to these guidelines and several contributions in the form of national or regional faunal treatments of some groups of Lepidoptera have been published recently for example of Peninsular Malaysia, Borneo, Thailand, Sulawesi, Sumatra, and Vietnam. On the same token, this volume is the third contribution to the knowledge of the insects of the Philippines with special emphasis on Lepidoptera within the Supplement series of "Nachrichten des Entomologischen Vereins Apollo", and it is an important addition to the taxonomy, nomenclature, and biogeography of the Lepidoptera.



This 576 page special issue is composed of 12 papers in English ranging from the physical description of the Philippines to annotated checklists of several lepidopteran groups and one of Trichoptera and descriptions of several new taxa. Ten of the 12 papers are devoted to Lepidoptera, therefore this issue is of special interest to the lepidopterist.

The following papers comprised the volume: "Short introduction to Philippine natural and geological history and its relevance for Lepidoptera" by C. G. Treadaway; "The Sphingidae (Lepidoptera) of the Philippines" by W. Hogenes and C. G. Treadaway; The Lasiocampidae (Lepidoptera) of the Philippines by V. V. Zohouhin, C. G. Treadaway and T. Witt; "The Saturniidae (Lepidoptera) of the Philippines" by W. A. Nässig and C. G. Treadaway; "The Brahmaeidae (Lepidoptera) of the Philippines" by W. A. Nässig and C. G. Treadaway; "Arguda sandrae" n. sp., a new lasiocampid (Lepidoptera: Lasiocampidae) moth from Palawan, Philippines" by A. Zwick; "Samia treadawayi (Lepidoptera: Saturniidae), a new species from Palawan Island, Philippines" by S. Naumann; "Two new species of the genus *Cyanosesia* Gorbunov & Arita, 1995 (Lepidoptera: Sesiidae) from the Oriental Region" by O. G. Gorbunov and A. Kallies; "The genus *Eoophyla* Swinhoe, 1900 (Lepidoptera: Crambidae: Acentropinae) from the Philippine Islands" by W. Speidel; The Scopariinae and Heliothelinae stat. rev. (Lepidoptera: Pyraloidea: Crambidae) of the Oriental Region—a revisional synopsis with descriptions of new species from the Philippines and Sumatra" by M. Nuss; "New records of *Cosmopterix* Hübner, [1825] (Lepidoptera: Cosmopterigidae) from the Philippines by W. Mey; "Contribution to the knowledge of the caddisflies (Insecta: Trichoptera) of the Philippines. 2. The species of the Mt. Agtuuganon Range on Mindanao" by W. Mey.

The issue starts with a brief, yet useful summary about the people, climate, forests, biogeography, and geological history of the archipelago. This general, introductory paper makes it easier to understand the rest of the papers, specifically the biogeographic and faunistic sections.

Four Lepidoptera families are thoroughly reviewed for the archipelago for the first time: Sphingidae, Lasiocampidae, Brahmaeidae, and Saturniidae; as well as the genus *Eoophyla* (Crambidae). The first of these papers is an annotated checklist of the Sphingidae known from the Philippines; 116 out of 117 species are illustrated in 18 color plates, including two new species and one subspecies. There is an analysis of the number of species and endemic taxa for each subfamily, tribe, and genus of Philippine Sphingidae; an evaluation of the richness and endemicity for the nine largest islands; and an evaluation of Sphingidae endemicity for each of Vane-Wright's faunal regions (R. I. Vane-Wright, 1990, *The Philippines—key to the biogeography of Wallacea?* Pp. 19–34. In Knight, W. J. and J. D. Holloway (eds.), *Insects and the rain forests of South East Asia (Wallacea)*, London, Royal Entomological Society, iv+343 pp.) The distribution of taxa is summarized in 23 maps. The next paper is an annotated checklist of the Lasiocampidae. Sixty-one species are noted from the Philippines, including one new genus, 18 new species and 6 subspecies; all illustrated in 12 color plates. The distribution of the species is figured in 34 maps, and the genitalia of most are illustrated in 13 black and white plates. In another contribution, 23 species of Saturniidae reported from the Philippine Islands (including 2 new species and 4 subspecies) are described, discussed, and illustrated in 13 color plates. In addition, pre-imaginal instars are depicted in 6 color plates. The male and female genitalia of most taxa are illustrated in 20 black and white plates; the known distribution of Philippine Saturniidae is presented in 16 maps. The degree of endemicity for each island and zoogeographical region is discussed. For the Brahmaeidae, the imaginal morphology, phenology, distribution, and variation of the only species present in the Philippines is thoroughly discussed. These papers will certainly be most often consulted by most lepidopterists, but the remaining six lepidopteran papers are providing important advances to our knowledge on Oriental Lepidoptera.

In three brief papers, a new lasiocampid, a new saturniid, and two new sesiids are described from the Philippines, respectively. The genus *Eoophyla* (Crambidae) from the Philippines is reviewed,

and two new species are described. Similarly, in the Cosmopterigidae two new species are described and two new records are reported for the country. On a more ample basis, the Scopariinae and Heliothelinae (Crambidae) of the Oriental region are reviewed; 11 genera and 63 species (including 6 new species) are recognized. This paper includes diagnoses and phylogenetic remarks for the higher taxa. In the last paper, a checklist of the fauna of caddisflies of the Mt. Agtuuganon Range on Mindanao is presented. An amazing number of 63 species out of the 102 listed are described and male genitalia illustrated for the first time.

It is important to note that special care was taken in order to insure accuracy in the localities used in the distribution discussions or maps. This is significant because specimens from commercial traders were usually collected or reared by local people on several islands, stored in the house of a Filipino trader with little or no data associated, imported to Europe, and then sold to customers. Thus, label data and the origin of most Philippine specimens in private collections (and probably in many museums) have been dubious as a result of the trade practices common in the area.

Very few criticisms can be made to this series of papers which are apparently free of misspellings and typographical errors. Although the maps are small, they are very clear, but the font size used for the species names make the legends almost illegible. In some cases the color photographs are too small and some have shadows that may hamper character observation.

This volume stresses the faunistics and taxonomy of Lepidoptera and contributes considerably to improve our knowledge of the Philippine insect fauna. This book is a must in the library of any individual interested in Sphingidae, Saturniidae, and Lasiocampidae in particular, or Oriental Lepidoptera in general. It should be present in all libraries that maintain coverage in entomology worldwide.

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THE AFROTROPICAL TIGER-MOTHS, by D. T. Goodger and A. Watson. 1995. Published by The Natural History Museum, London, and Apollo Books. 65 pp., 4 color plates of adults, 109 black-and-white photographs of genitalia. Softcover, 29.6 × 21.0 cm, ISBN 87-88757-32-3. Available from Apollo Books Aps., Kirkeby Sand 19, DK-5771, Stenstrup, Denmark, Tel. 45-62-26-3737 FAX: 45-62-26-3780. Price DDK 200.00 (approximately U.S. \$32.00).

The purpose of this book, in the authors' words, is to serve as an illustrated catalogue, with generic diagnoses and species distribution of the currently recognized and described afrotropical Arctiinae. The layout of the work is straightforward and easy to follow. There is a brief synopsis, introduction, comments on the structure of the catalogue entries, as well as a list of genera and species removed from the Arctiinae, followed by the main body of the catalogue, which occupies some 20 pages.

In the catalogue, generic entries are kept short and concise, and generally follow the pattern established in the well-known series *Generic Names of Moths of the World*. Information provided includes the name, author, date of publication and pagination, followed by a similar statement on the type species. Also listed are junior synonyms and homonyms.

The entries on species include, again, the name, author, date of publication and pagination, and a statement (in parentheses) of the genus in which the taxon was originally published. Oddly, in the many cases where species were subsequently transferred to another genus, the authors do not indicate this by placing author and year in parentheses. The only explanation I can think of is that this was done in order not to interrupt the flow of text as the pagination is given immediately after the year (e.g., in an entry under *Alpenus* Walker:



*affiniola* Strand, 1919:168 (*Diacrisia*)). Whatever the reasoning, this manner of citation is confusing and violates article 51(c) of the International Code of Zoological Nomenclature [Article 51(c) states: "If a species-group name is combined with generic name other than the original one, the name of the author of the species-group name, if cited, is to be enclosed in parentheses"]. Further information provided in the species entries includes a brief statement about the nature of the type material and a similarly brief indication of distribution. Inset appear junior synonyms, homonyms, incorrect spellings, or infrasubspecific names.

A further irritation to me was the disregard shown to articles 31(b) and 34(b), dealing with the of late much-discussed problem of agreement in gender [Article 31(b) states: "A species-group name, if it is or ends in a Latin adjective or participle in the nominative singular, or is latinized, must agree in gender with the generic name with which it is at any time combined, and its termination must be changed according to Latin inflection, . . ."; Article 34(b) states: "The termination of a Latin or latinized adjectival or participial species-group name must agree in gender with the generic name with which it is at any time combined; if the termination is incorrect it must be changed accordingly (the author and date of the species-group name remain unchanged Arts 50c(ii), 23c"). This is especially obvious in cases such as the species-rich genus *Spilosoma*, which, despite its ending, is in fact neuter. I am well aware that many readers of these lines will argue that I am nit-picking and many of the rules governing the use of the classical languages have become obsolete. I disagree, but even if I did not, the Code is quite unambiguous about the matter.

Following these entries (said to cover 411) are listed the 20 genera and their constituent species removed from the Arctiinae. This section has the same layout as the main catalogue. Most of these genera are now placed in the Noctuidae, and it is a pity that no indication is given of the subfamilies to which they are likely to belong, as this would have made making changes much easier. Given the more than doubtful monophyly of many noctuid subfamilies, however, it seems quite possible that their affinities are simply not known.

The text is complimented by a list of recorded hostplants of afrotropical tiger-moths and a bibliography with some 311 entries.

The four color plates of adults are of high quality and depict mostly type species. Similarly, the black-and-white photographs illustrate the male genitalia mostly of type species. Here, depth of field is occasionally lacking, although this is hardly surprising given the frequently robust genitalia in this family.

All in all, this little book will serve as a useful introduction to, and overview of, this beautiful group of moths in the afrotropics. Its main strengths lies in its conciseness, but I feel it would have profited from a little more attention to detail.

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THE MOTHS OF AMERICA NORTH OF MEXICO, fascicle 27.3, Noctuoidea, Noctuidae (part), Noctuidae (part Noctuini), by J. D. Lafontaine. 1998. Published by the The Wedge Entomological Research Foundation, Washington, D.C. 348 pp., 8 color plates. Soft cover, 8 × 11 inches, ISBN: 0-933003-09-9. Available from The Wedge Entomological Research Foundation, 85253 Ridgetop Drive, Eugene, OR, 97405, USA. \$115.00+postage (\$4.00 U.S., \$5.00 elsewhere). Also available from Bioquip Products and Entomological Reprint Specialists.

In October 1998, someone asked about the classification of the Lepidoptera via the Internet. Several persons replied: "There is no one universally agreed upon classification." The classification of

Lepidoptera is not cast in stone, nor will it be anytime in the near future. Don Lafontaine's superb work exemplifies the answer given above. The Board of Editors of *The Moths of America North of Mexico* series, affectionately known as MONA, deserves recognition for advancing classifications rather than casting one system in stone.

This is the second fascicle of the MONA series, artfully written by Lafontaine, on part of the Noctuini with a discussion on the classification of the tribe. He plans a third fascicle on the tribe Agrotini. Such facts would be simple except that a previously published fascicle of the MONA series by Robert W. Poole (1995, *Noctuoidea, Noctuidae (part)* in Dominick, R. B. et al., *The Moths of America North of Mexico*, fasc. 26.1:1–249) proposed a classification that significantly altered the definition of the subfamily Noctuinae. I don't know if either classification is correct, but I am very pleased that the MONA series can be fodder for discussions about the classification of Lepidoptera, in addition to producing excellent monographic works. I seek knowledge, I love to learn, and the MONA series—well amore!

Most aficionados of Lepidoptera are already familiar with the MONA series. It is recognized for its high quality, authoritative look at moths, and perhaps best of all, the fascicles introduce and illustrate little known species, thus popularizing the study of moths. Lafontaine's fascicle does not let us down.

The volume starts with a morphological, systematic, and taxonomic overview of the group. One hundred sixty-nine species in 31 genera are included. Four new genera are proposed and 21 new species are described. Many new combinations are presented. Revised nomenclature abounds. Complete citations are provided for persons to fully understand Lafontaine's overview and philosophy. Drawings supplement the morphological descriptions. The bibliography is rich with entries.

A subtle digression from MONA's perceived format is the inclusion of three species from Mexico. This important change allows the author to more fully describe and explain his groupings, and the reader will recognize these species if one day they are found to be part of the U.S. fauna. Lafontaine makes full use of keys to genera and species, a feature I find especially helpful when I want to know how the author differentiates taxa.

Lafontaine is an excellent writer. His verbiage is succinct and lucid. Overviews and details are sufficient to allow a reader to understand the text, which is, as always, beautifully elucidated with illustrations of genitalia, adults, larvae, and distribution maps. All of the illustrations are superior to what can commonly be found in scientific publications. My grammar teachers would disagree with the structure of only a couple of sentences.

An extremely unfortunate trend in the book binding industry provides my only criticism of this volume. Breaking with tradition of the MONA series, this book is not Smythe sewn, rather it is perfect bound—which is in my opinion, highly imperfect. Smythe sewing is expensive, and as binders become convinced of the invincibility of glue, there are fewer binders who use the superior Smythe sewing. For persons who bind their books in buckram, as do I, perfect binding creates cramped inner margins and books that will not lie flat open. Persons who do not bind their books will also notice that this volume will not gracefully lie flat when opened. I cannot predict that pages will fall out; time and use will test the glue.

I don't want anyone to miss the point that I give Lafontaine's work, and this volume high marks. All persons interested in the Noctuidae, on a worldwide basis, will need this information. This book will be a standard for a long time because it treats so many species of economic importance, i.e., cutworms. Other persons should be familiar with this work so that they can explore the analysis, fully explained by Lafontaine, employed in writing a revision of this magnitude. I highly recommend it. Any person interested in moths should own a copy.

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SATURNIIDAE MUNDI: SATURNIID MOTHS OF THE WORLD, Part 3, by Bernard D'Abrera. 1998. Published by Goecke & Evers, Sportplatzweg 5, D-75210 Keltern, Germany (email: entomology@s-direkt.net.de), in association with Hill House, Melbourne & London. 171 pages, 88 color plates. Hard cover, 26 x 35 cm, dust jacket, glossy paper, ISBN-3-931374-03-3, £148 (about U.S. \$250), available from the publisher, also in U.S. from BioQuip Products.

Imagine a large book with the highest quality color plates showing many of the largest and most famous Saturniidae from around the world! Imagine that this book shows males and females of all the 14 known species of *Attacus*, in addition to the equally massive *Coscinocera* and *Archaeoattacus*. Imagine that all of the American *Rothschildia* were depicted, as well as all of the African *Epiphora*. Imagine many of the species of *Samia*, some recently discovered in and described from Indonesia and China, to be included. Imagine that the North American *Callosamia*, *Hyalophora*, and *Eupackardia* were included to complete the tribe Attacini. Imagine that this book had all of the beautiful *Actias*, *Argema*, and *Graellsia*, with their delicate green, yellow, and pink coloration, and tailed hindwings. Now suppose such a book included all species of the confusing and complex group from the Northern Hemisphere usually placed in *Saturnia*, *Caligula*, *Neoris*, *Agapema*, *Eriogyna*, and *Perisomena*, all neatly sorted out and figured. Add to all these, numerous other saturniids in well-known genera like *Rhodinia*, *Loepa*, *Copaxa*, and *Cricula*, and lesser-known genera like *Syntherata*, *Opodiphthera*, *Lemaireia*, and *Pararhodia*. If you can imagine all of those saturniids shown as life-sized illustrations, then you can begin to visualize the satisfaction that this book will bring to everyone who owns or uses it. This is the book for which lepidopterists who love Saturniidae have been waiting!

The book shows many species that are absent from most museum and private collections. For example, from China is shown the rich maroon colored *Samia watsoni*, the massive peach-colored *Loepa oberthuri*, and *Actias dubernardi*, the most gracile of all the *Actias*. From East Africa is the unique *Argema besanti*, the smallest yet perhaps the most beautiful of its genus, and from Indonesia we see *Samia yayukae*, *Samia naumanni*, and *Cricula hayatia*. Included also are several recently described species such as *Neoris codyi* from Pakistan, named for the American saturniid artist John Cody, *Opodiphthera excavus* from Queensland that forms its cocoons below ground to avoid sweeping fires, *Samia treadawayi* from the Philippines, *Actias angulocaudata* and *Loepa obscurumarginata* both from China, *Agapema platensis* from Texas, *Copaxa evelynae* from Guatemala, and *Rothschildia renatae* from Peru. None of the latter three species could be included in Claude Lemaire's revision of the American representatives of the subfamily Saturniinae (1978, *Les Attacidae Américains*, Édition C. Lemaire, Neuilly-sur-Seine, France, 238 pp., 49 pls.), because they had not yet been discovered in 1978.

I will provide some taxonomic commentary. In the book, D'Abrera describes two new species: *Opodiphthera goodgeri* and *Pararhodia setekwa*, both from New Guinea. The figure of *Actias chapae* from Chapa, Vietnam (near its northern border with China), shows that it is a very distinct species; I had not seen a figure or specimen of *A. chapae* until now. The figure of the Chinese *Actias felix* still makes me think that this name is a synonym of *A. gnoma* from Japan and Siberia, an opinion I reached long ago. The taxonomic differences between *Actias heterogyna* and *A. sinensis* are not clear in the figures in this book. D'Abrera has shown good insight by sorting out some synonymies in *Epiphora* and *Coscinocera*. We now have a color figure of each pair of species of *Opodiphthera*, enabling

us to identify material from New Guinea in the *sciron* group, which includes several species that look much alike. Prior to this we only had a key published by E.-L. Bouvier (1936, *Mem. Natl. Mus. Nat. Hist. Paris*, 3:1–350), in which he called these species *Neodiphthera*. I agree with D'Abrera's interpretation of the distribution of *Attacus aurantiacus*.

As with D'Abrera's similar books on Sphingidae and butterflies, this one is a pictorial guide to these moths, based largely on specimens in The Natural History Museum in London. In an effort to make the coverage as complete as possible, the author has done an exceptional job of gathering missing material to be photographed, receiving several loans and donations from Australia, Belgium, France, Germany, and the United States. He has largely succeeded; relatively few known species are missing. Missing also, but by design, is the extensive genus *Antheraea*, because it will be treated in Part 2 along with the many African genera such as *Imbrasia*, *Pseudoburnaea*, *Gynanisa*, *Eochroa*, *Heniocha*, *Usta*, *Eustera*, *Ludia*, and *Microgona*. Part 1 of *Saturniidae Mundi* was published in 1995 (reviewed in 1996, *J. Lepid. Soc.* 50(4):355–356) and included the magnificent moths in the genera *Copiopteryx*, *Arsenura*, *Automeris*, *Hemileuca*, *Citheronia*, *Eacles*, and related groups.

In Part 3, the text is not very extensive for each species, mainly giving the citation to the original description, diagnostic characters, and the distribution in general terms. An additional component is that for many species D'Abrera refers the reader to primary sources in literature where the life history and immature stages have been described and figured by other authors. D'Abrera does not use subgenera and makes minimal use of the subspecies category, thereby preserving the most basic tenets of the binomial system of nomenclature intended by Linnaeus. My taxonomic philosophy is in total agreement with his approach. D'Abrera's taxonomy is both conservative and accurate. I found virtually no errors in spelling or fact. The book is extremely reliable as an authoritative source on these venerable moths.

As in Part 1, the introductory section offers some photographic portraits of some of those who contributed significantly to our knowledge of Saturniidae in the past, and who are actively doing so in the present. These include Charles Oberthür, Dr. Karl Jordan, Walter Rothschild, Dr. Stefan Naumann, Captain Ulrich Paukstadt, Laela Hayati Paukstadt, and Thierry Bouyer.

All who consider Saturniidae to be among their special interests will want this book, but some will delay or avoid purchasing a copy because of the high cost. A book of this magnitude and physical quality simply cannot be sold these days for less money. Publishers and authors are not getting rich on these kinds of publications. Anyone who considers the price to be an obstacle should buy this one book instead of spending more money in the long run trying to buy several other books (some of which are out of print and hard to find) that still would not show as many color figures of saturniids. With a print run of only 1500 copies, I would not wait too long to buy one. Most of us will never be able to obtain most of the species shown in this book for our collections, no matter how intensively we collect, buy, and exchange specimens. However, we can have a complete collection of these moths in the form of fine color figures. For amateurs who rarely have the opportunity to see the foreign literature on Saturniidae, current and historical, this volume offers the best and really the only opportunity to become knowledgeable about the names of the many species that exist, where they are from, and what they look like. I highly recommend this book because it will prove to be both immensely useful and a true pleasure to own. It represents a milestone in the literature on Lepidoptera.

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**Cover illustration:** *Antheraea montezuma* (Sallé) (Saturniidae), male. A close relative of *A. polyphemus*, this species flies throughout much of Mexico. Pen and ink drawing by John T. Carrola Jr., University of the Incarnate Word, San Antonio, Texas.

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## A TECHNIQUE FOR EXTRACTION OF INTACT MITOCHONDRIAL DNA MOLECULES FROM LARVAE OF SATURNIID MOTHS (LEPIDOPTERA: SATURNIIDAE) FOR USE IN TAXONOMIC STUDIES

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**ABSTRACT.** Analysis of mitochondrial DNA can yield information about evolutionary relationships. In this paper, a set of procedures for the extraction and analysis of mtDNA from saturniid moths is described. Restriction fragment length polymorphisms reveal differences in the mtDNA of the species investigated. The potential of this methodology to contribute to comparative studies of moth species is discussed.

**Additional key words:** *Hyalophora*, *Callosamia*, RFLP, taxonomy, phylogeny.

The use of mitochondrial DNA (mtDNA) in studies of taxonomic and evolutionary relationships in insect groups has become well established since Bultman and Laird (1973) extracted, purified and described the physical characteristics of mtDNA from *Drosophila melanogaster* Meigen. Brower and Boyce (1991), Sperling (1993), Sperling and Harrison (1994), and Brower's (1994) extensive taxonomic and phylogenetic studies on butterflies are examples of the application of mtDNA organization to phylogenetic studies of Lepidoptera.

I became interested in carrying out mtDNA studies and began to learn the basic techniques of mtDNA extraction, purification and analysis. I chose to work with the genus *Hyalophora* Duncan (Lepidoptera: Saturniidae) because I had been rearing and studying *H. cecropia* (L.) and *H. columbia gloveri* Strecker for many years. The several species, subspecies and hybrid populations of the genus occur in geographic areas that are distinct from each other but overlap (Scriber & Grabstein 1991, Collins 1997). They also show food preferences and thus occupy slightly different niches (Oberfoell 1969, Scriber & Grabstein 1991, Collins 1984).

The genus *Hyalophora* is presently considered to consist of three species: *H. cecropia* L., *H. columbia*

Smith with the subspecies *H. columbia gloveri* Strecker and *H. columbia columbia* Smith; and *H. euryalus* Boisduval with one subspecies, *H. euryalus cedrosensis* Cockerell. This last subspecies, found only on the Isla de Cedros, Baja California, Mexico, was thought to be extinct until rediscovered and described by Smith and Wells (1993).

This organization of the genus was developed by Lemaire (1978) and reflects the studies of zones of hybridization between *H. euryalus* and *H. columbia gloveri* carried out by Sweadner (1937), repeated and extended by Collins (1973) and Kohalmi and Moens (1975, 1988). It is the classification used by Tuskes et al. (1996) and by Collins (1997).

Molecular evolutionary studies of saturniids include those of Collins et al. (1993) whose analysis of the distribution of 20 allozymes confirmed the hybrid nature of populations where *H. euryalus* and *H. columbia gloveri* came in contact with each other. Legge (1993) used DNA primers for the cytochrome oxidase II (COII) gene, in conjunction with polymerase chain reaction (PCR) amplification, to isolate COII genes from total genomic DNA of several species of Hemileuca. Legge (1993) was able to use the nucleotide sequences of COII genes to construct consensus trees for phylo-



genetic analysis of species of the genus *Hemileuca*. Friedlander et al. (1998) used the sequence information of two nuclear genes to construct consensus trees showing the phylogenetic relationships of species of the Attacini, including the three *Hyalophora* species, and the Saturniini.

To my knowledge, no one has yet reported the isolation of complete mtDNA molecules from Saturniid species. Having the complete molecule would be an asset to anyone investigating phylogenetic relationships between moth species. It turns out that the moth tissue having the greatest quantity of mitochondria is the gut of mature larvae. Anderson and Harvey (1966) studied the fine structure of the *H. cecropia* midgut epithelium and found that both the microvillae which extended into the gut lumen and the channels formed by the deep infoldings of the apical and basal plasma membrane were packed with mitochondria. This rich source of mitochondria was used to initiate a comparative study of the mtDNA of *Hyalophora* species. In this paper I present the methodology developed and some initial results of this study.

#### MATERIALS AND METHODS

All glassware, Eppendorf tubes, pipet tips and solutions are autoclaved prior to mtDNA processing. Items that are going to be reused are washed in hot water containing Alconox™ detergent, then rinsed in tap water, followed by a rinse in deionized water. These are air dried, placed in glass containers which are capped with aluminum foil, and autoclaved for 30 min at 120°C. Plastic gloves are worn during extraction procedures to reduce the chance for contamination of the mtDNA.

Mitochondria are taken from the guts of healthy 4<sup>th</sup> or 5<sup>th</sup> instar larvae which have been cleaned of their contents. The larvae used for this study were reared from ova deposited by 15 *H. cecropia*, 8 *H. columbia columbia*, 2 *H. columbia gloveri*, 7 *H. euryalus*, and 2 *Callosamia promethea* Drury. The last were used as an outgroup. The sources of ova are listed in Table 1.

Larvae, except as noted below, are laboratory reared in plastic sweater boxes on fresh leaves of cherry (*Prunus* sp.) or white oak (*Quercus alba* L.) which have been sprayed with an antibiotic solution (Riddiford 1967). The number of larvae per box is kept small and larvae are handled as little as possible. *H. columbia* are reared on branches of *Larix laricina* (DuRoi) K. Koch.

Mature larvae are anesthetized under carbon dioxide gas, decapitated and severed near the posterior. The body wall is cut through along the ventral side and the larva is pinned out. Next, the gut is cut longitudi-

TABLE 1. Suppliers of the ova used in this research.

Moth species	Supplier
<i>H. cecropia</i>	+ Ralph M. Clark, Plattsburgh, NY Larry Kopp, Klingerstown, PA + * James Oberfoell, Bowman, ND Mark Schmidt, Springboro, OH Scott Smith, Santa Rosa, CA
<i>H. euryalus</i>	+ Dean Morewood, Victoria, BC, Canada + Norman Smith, Fresno, CA Scott Smith, Santa Rosa, CA
<i>H. columbia columbia</i>	Gardiner Gregory, Orland, ME William Kenny, Dixmont, ME ° Mark Schmidt, Springboro, OH + Ted Herig
<i>H. columbia gloveri</i>	+ * James Oberfoell, Bowman, ND Mark Schmidt, Springboro, OH Scott Smith, Santa Rosa, CA
<i>A. polyphemus</i>	Mark Schmidt, Springboro, OH
<i>C. promethea</i>	Larry Kopp, Klingerstown, PA Mark Schmidt, Springboro, OH

+ Native moths reared by supplier from representatives of local populations.

\* Present address unknown.

° From stock supplied by W. Kenny.

nally along its ventral side and the gut contents are removed. In the best of cases, the peritrophic membrane can be lifted and rolled forward to remove the gut contents cleanly. The tracheal trunks that serve the gut are severed. The gut is removed from the body cavity, washed thoroughly in deionized water and transferred to containers chilled in ice or dry ice. Most tissues are weighed and stored at -70°C within the hour. Each sample consists of 4 or 5 guts. These samples are processed to extract mtDNA as soon as possible. Tissues that are to be processed immediately are transferred to a chilled Wheaton dounce homogenizer which contains 5 ml of a physiological buffer (0.44 M sucrose, 0.01 M Tris, 0.18 mM EDTA; pH 7.5). Tissues in the dounce, either fresh or frozen, are macerated and the mtDNA is extracted using a procedure described by Tamura and Aotsuka (1988), with the modifications given below.

Differential centrifugation in a physiological buffer is followed by alkaline lysis of the mitochondrial fraction. A centrifugation step separates the mtDNA from cellular debris and the mtDNA is further purified by phenol extraction. The mtDNA is precipitated from an alcoholic solution, resuspended in T<sub>10</sub>E<sub>1</sub> and treated with the enzyme, RNase, before storage at -20°C.

Standard endonuclease digestions are carried out using a variety of endonucleases. A digest of lambda DNA with Hind III is used to generate a reference kilobase pair (Kbp) ladder against which to size restriction fragments. The digests are loaded into the wells of 1% agarose (GIBCO/BRL) gels. Electrophoresis is carried out in a Hoefer Scientific Instru-

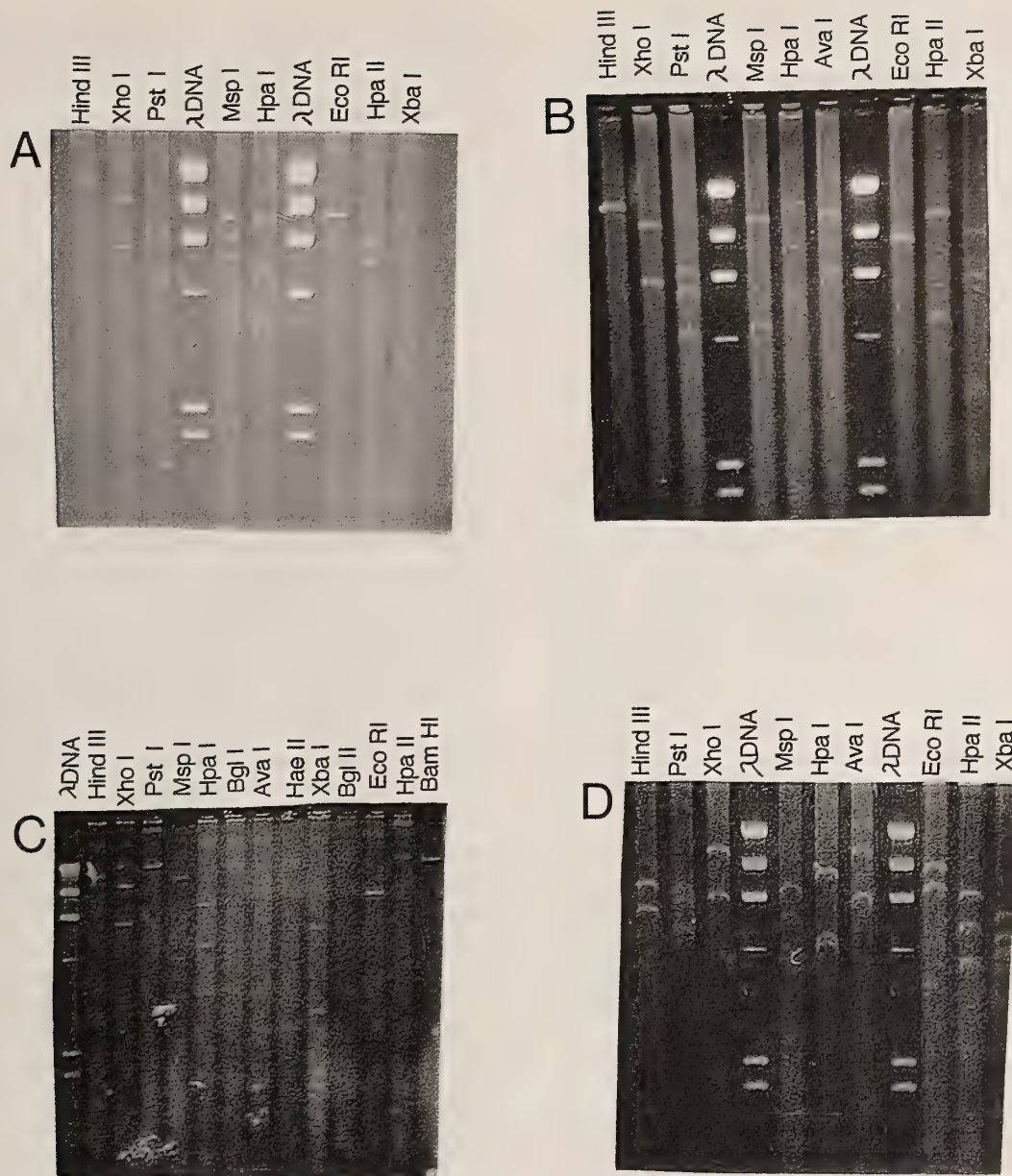


FIG. 1. Representative electrophoretic patterns for A) *H. columbia columbia*; B) *H. euryalus*; C) *H. cecropia*; and D) *C. promethea*.

ments unit set at 37V, 23 milliamps. TBE is the electrophoretic buffer. The gel slab is stained with ethidium bromide, then destained in 0.1 mM  $\text{MgSO}_4$  before examination under ultraviolet light. Gels are photographed and common pins are positioned in the gel to mark the position of mtDNA fragments. Measures of distances of the pins from the wells are taken and used to construct gel replicas and to determine the sizes of the mtDNA fragments in kilobase pairs (Kbp).

## RESULTS

The photographs in Fig. 1a, b, c, d are examples of electrophoretic patterns obtained when mtDNA from larval guts is digested with these endonucleases. A number of bands the size of the largest  $\lambda$ -DNA fragment or larger is seen in Fig. 1c. These are taken as evidence of incomplete digestion; the presence of non-mt-DNA in the sample, and/or from complexes



TABLE 2. Number of endonuclease sites observed in mtDNA of four saturniid species for the listed enzymes.

Species	Enzyme			
	Hind III	Msp I (Hpa II)	Hpa I	Pst I
<i>H. cecropia</i>	3	2	3	2
<i>H. columbia</i>	3	3	3	3
<i>H. euryalus</i>	3	2	2	3
<i>C. promethea</i>	2	3	3	3

formed when the DNA concentration in a sample is excessive.

The patterns of cleavage for these species are very consistent. Not shown is the pattern for *H. columbia gloveri* which is identical to *H. columbia columbia*. Eight of the endonucleases tested to date yield information useful for phylogenetic analysis. These are Hind III, XhoI, PstI, MspI, EcoRI, AvaI, HpaI and HpaII. The isoschizomers MspI and HpaII have identical cleavage patterns indicating that the cytosines of 5-CCGG-3 sequences are not methylated. XbaI results are very inconsistent. This enzyme is known for aberrant cleavage if exact reaction conditions are not followed (Gibco/BRL 1997-98 Catalog). Among the endonucleases that do not cleave these saturniid mtDNAs are BglI, HaeII, BglII and Bam HI (Fig. 1c).

Species specific differences in cleavage patterns are observed when the photographs in Fig. 1 are compared (Table 2). There are no observed differences in the number of cleavage sites for the other endonucleases. The two small Hind III cleavage sites are about 2.2 and 1.7 kilobase pairs (Kbp) long and difficult to see as they stain faintly with ethidium bromide, and photograph poorly.

The single band seen when *Hyalophora* mtDNA is cut by EcoRI (Figs. 1a, b, c) is judged to be about 920 Kbp long, based on its position relative to the 960 Kbp band of the  $\lambda$ -Hind III standard. Since all my results indicate that moth mtDNA is between 14-19 Kbp in length (a size range common to animals), EcoRI apparently cuts the mtDNA in two places which yields two fragments of approximately equal size. The two fragments comigrate. The *C. promethea* mtDNA is also cut at two locations by Eco RI, but the product is two fragments of unequal size, thus there are two bands (Fig. 1d). The size of these two fragments totals to about 16 Kbp. This is one of two examples seen where RFLPs result from an internal reorganization of mtDNA, not from the gain or loss of the number of enzyme sites. A second example is seen when the HpaI digest pattern of *C. promethea* is compared to the hyalophorans (Fig. 1).

TABLE 3. Haplotypes of species of *Hyalophora* and *C. promethea* based on electrophoretic patterns after digestion of mtDNA with the listed enzymes. *H. cecropia*'s haplotype is used as the basis for comparison. RFLPs are indicated by letter changes. The two sub-species of *H. columbia* exhibit identical haplotypes.

Species	Enzyme						
	Hind III	Msp I (Hpa II)	Hpa I	Pst I	Ava I	Xho I	EcoRI
<i>H. cecropia</i>	A	A	A	A	A	A	A
<i>H. columbia</i>	A	B	A	B	A	A	A
<i>H. euryalus</i>	A	A	B	B	A	A	A
<i>C. promethea</i>	B	B	C	B	A	B	B

Table 3 presents the haplotypes of the species studied, based on RFLPs. If one elects the *H. cecropia* haplotype as the base against which to compare the others, then one can see that the *H. cecropia* restriction pattern differs from *H. columbia* and *H. euryalus* for two of seven enzymes, but not the same enzymes; from the *C. promethea* haplotype for 5 of 7 enzymes.

*H. columbia* haplotypes show two mtDNA modifications from *H. euryalus* and three from *C. promethea*. *H. euryalus* differs from *C. promethea* at five sites, but not the same five by which *C. promethea* and *H. cecropia* differ. The PstI digest pattern of *H. cecropia* is unique.

Most of these polymorphisms are caused by the gain or loss of sites for enzyme attack, however the uniqueness of the *C. promethea* haplotype may result from RFLPs created by internal rearrangements of the mtDNA (HpaI and EcoRI digests).

## DISCUSSION

The major reason for this paper is to present procedures for the extraction, partial purification and analysis of complete molecules of moth mtDNA. This has been accomplished by adapting procedures of others to the extraction of mtDNA from the guts of mature moth larvae. The results show that larval lepidoptera are good sources of mitochondrial DNA for use in studies of taxonomy and phylogeny. Even though the mtDNA obtained using this methodology was not highly purified, and even though the electrophoretic stain used was not the most sensitive, results are quite reliable. Distinct RFLPs and haplotypes of the four saturniid species were observed.

Contamination of the mtDNA with nuclear DNA was not a problem. Tamura and Aotsuka (1988) stated that the purity of mitochondria as a result of differential centrifugation is not important because the alkaline lysis procedure efficiently separates covalently closed circular mtDNA from linear DNA. Legges' (1993) concern that mtDNA from gut tissues could be seriously contaminated by gut organisms are allayed by



the results presented here. By using the procedures of Jones et al. (1988) greatly improved purification and fragment resolution is possible.

The advantage of this method over that utilized by Legge (1993) and others to obtain and sequence the *CoII* gene is that the entire mtDNA molecule is obtained. This allows studies of RFLPs and the construction of restriction maps of the mtDNA chromosome based on double-digest studies. Additionally, sequencing of entire mtDNA molecules is possible. The results of such studies will reveal any internal rearrangement or mutations of the mtDNA molecule that is species or population specific. Two such internal rearrangements have been discovered during this study (Table 3). Sequencing of the entire molecule may reveal any introgression of genetic sequences where hybrid zones exist. Kondo et al. (1990) presented clear evidence of heteroplasmy in *Drosophila* and the occurrence of introgression of mtDNA. Introgression of mtDNA in *Drosophila* was also observed by Aubert and Solignac (1990). If introgression is found in natural hybrid zones it could reveal cross-overs between native and introduced mtDNAs and help clarify evolutionary relationships within *Hyalophora*. It could also reveal the existence or establishment of subpopulations within a population by revealing two or more maternal lineages that are established through reciprocal crosses.

Table 3 is based on a system used by Avise and Nelson (1989) to illustrate relationships between the genomes of seaside sparrows that were dispersed over a wide geographic area of the southeastern United States. I have adapted this system as it seems to illustrate haplotype differences most clearly.

The distinctness of the *C. promethea* mtDNA from that of *Hyalophora* is readily apparent as 3 of the 7 enzymes used to digest the samples yield results that are unique to *C. promethea*. This pattern would suggest a separate line of evolution for the *Callosamia* and would corroborate the findings of Friedlander, et al. (1998) and Johnson, et al. (1996). One can infer that the identity of the digest patterns of the two subspecies of *H. columbia* indicates that these two are more closely related to each other than they are to the other *Hyalophora*. Also, the *PstI* digest pattern which is unique to *H. cecropia* suggests an evolutionary separation from the others, with the *PstI* pattern of *C. promethea* possibly being more ancient and unchanged in columbians and euryalus. However one must be aware that both forward and reverse mutations occur.

There is not enough information here to make further inferences as to the degree of relatedness and lines of evolution of the *Hyalophora*. However, nothing in these results contradict the findings of Sweadner

(1937), Lemaire (1978), Tuskes, et al. (1996) or Collins (1973, 1997). It would be interesting to have samples of *H. euryalus cedroensis* mtDNA to study because of its potentially long-time isolation from the rest of the *Hyalophora*. The naming of the two *H. columbia* subspecies creates confusion because even though *H. columbia gloveri* is believed to be ancestral to *H. columbia columbia* (Sweadner 1937, Collins 1997), the *H. columbia* name has priority.

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A NEW SPECIES OF *LITHOPHANE* (LEPIDOPTERA:  
NOCTUIDAE: CUCULLIINAE) FROM NORTHEASTERN NORTH AMERICA

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**ABSTRACT:** A new species of noctuid moth is described and illustrated. *Lithophane thujae*, **new species**, is known from two localities in New Brunswick, Canada, and one locality each in Michigan and Wisconsin, U.S.A. The probable larval host plant is northern white-cedar (*arbor vitae*), *Thuja occidentalis* L. (Cupressaceae). Notes on its biology are given and the last instar larva is figured.

**Additional key words:** Winter moths, *Lithophane lemmeri*, New Brunswick, Michigan, Wisconsin.

In late April 1990 a female specimen of an unusual *Lithophane* was collected at mercury vapor (M.V.) light by the authors a few km south of Harvey Station, York Co., New Brunswick. This specimen was tentatively identified as *Lithophane* species near *lemmeri* Barnes & Benjamin by Donald Lafontaine of the Biosystematics Laboratory, Ottawa, Canada. Another female of this species was collected at M.V. light by the senior author near Fredericton, York Co., N.B., in early June 1992. Eggs were obtained from this female and neonate larvae were given a choice of 21 species of woody shrubs and trees from the area where the moth was collected. The larvae refused to feed on the foliage of all species except northern white cedar, *Thuja occidentalis* L. (Cupressaceae). Larvae were reared on the foliage of *T. occidentalis*, and adults were produced in late September, 1992. Additional specimens were reared in 1996 from another female collected at the locality near Fredericton in early May at M.V. light. Another two specimens of this species from Michigan and one from Wisconsin were located in the respective collections of Mogens C. Nielsen and James C. Parkinson. These had been identified as *Lithophane* new sp. near *lemmeri* by Dale F. Schweitzer. Comparison of the male genitalia of these moths to those of *L. lemmeri*, which occurs along the Atlantic coast of the U.S.A., demonstrated that this *Lithophane* was not conspecific with *L. lemmeri*. We therefore describe this insect as a new species.

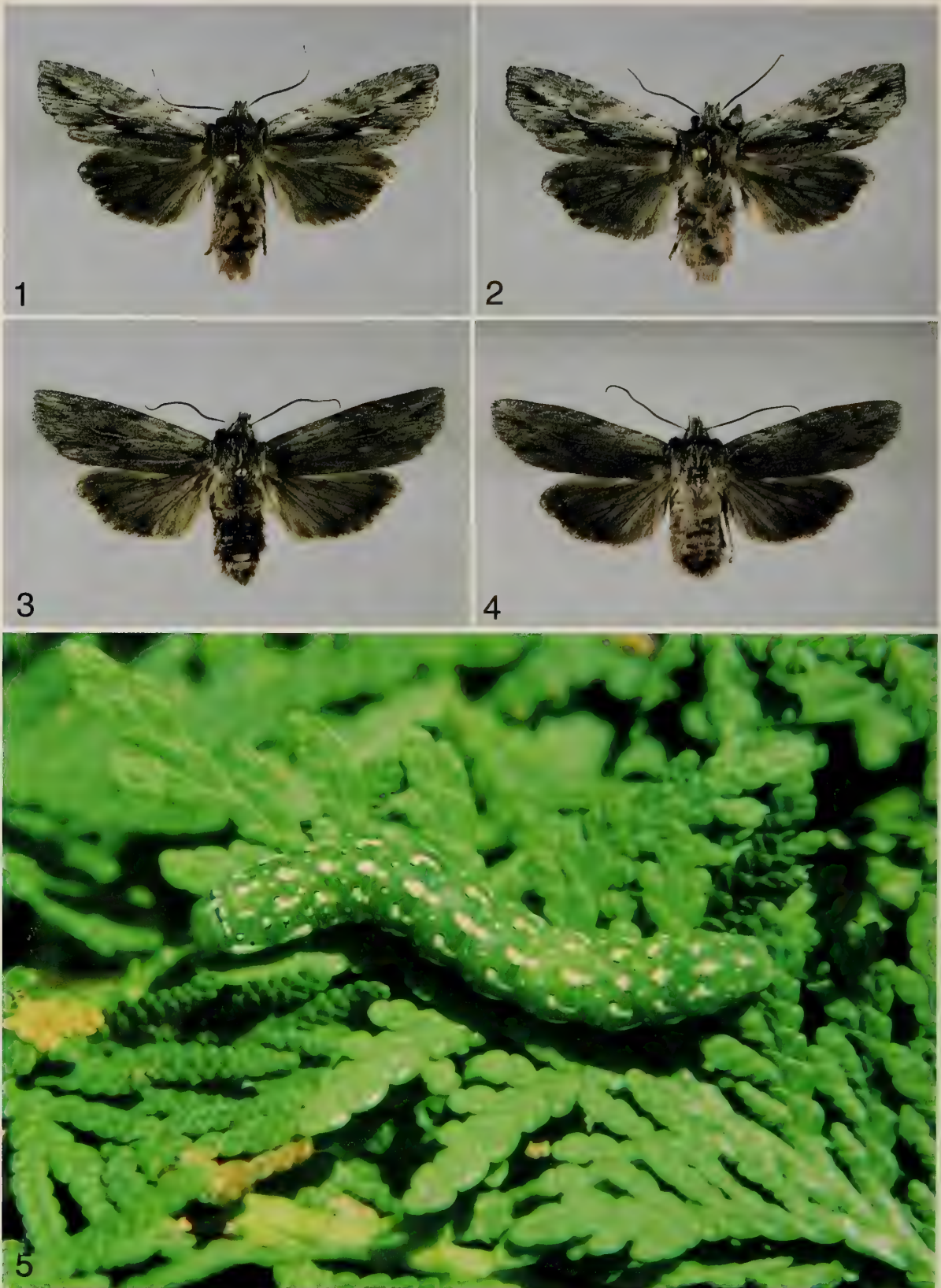
*Lithophane thujae* Webster and Thomas,  
**new species**  
(Figs. 1, 2, 6, 7)

**Description** (Figs. 1 and 2). Forewing narrow, length 16.0–18.1 mm (mean = 17.2), width at tornus 6.0–7.5 mm (mean = 7.0) (n = 24) in males and length 16.0–18.5 mm (mean = 17.3), width at tornus 6.0–8.0 mm (mean = 7.2) (n = 46) in females. Anterior half of

termen at nearly right angle with distal 1/3 of costa, then angled inwards toward tornus at approximately a 135° angle; lower half of termen slightly emarginated above tornus. Forewing above brownish gray grading to light gray near the anterior margin basally and brown with pinkish hue along posterior margin becoming salmon pink near base of wing. Reniform spot indistinct, dirty salmon pink, basal portion contrasting with lighter gray anterior portion. Orbicular spot absent. Basal dash consists of thin black line. Thicker black median streak between indistinct antemedial and postmedial lines, and well developed subreniform black line outlined anteriorly with white. Apical dash small, black and subterminal line indicated by series of 4 black dashes, most anterior connected to brownish apical streak. Hindwing above darker than forewing and grayish brown with salmon pink hue, discal dot faintly expressed. Fringes of both wings concolorous with adjacent portions of wing. Underside of fore- and hindwings uniformly light gray with strong salmon pink tint except for darker central area of forewing. Discal spot on underside of hindwing well developed. Color and pattern similar in both sexes and uniform among specimens examined. Dorsal side of thorax gray with mid-dorsal brown patch bisected by fine white line extending from collar to base of abdomen. Tegula elongated and gray, margined with black above wing base. Anteriorly, mesothoracic vestiture terminates in V-shaped crest. Patagium concolorous with tegula, but bordered posteriorly towards mid-line by fine black line followed by white line. These lines on adjacent patagia form a V, opening formed by thoracic crest which emerges between arms of V. Head vestiture, dorsally, concolorous with patagia and tegulae. Palpi and ventral thorax gray with definite pinkish hue. Dorsally, abdomen gray with pinkish hue and without tufts; ventrally abdomen approaches dirty salmon pink. Prothoracic legs entirely dirty salmon pink. Outer lateral portions of femur and tibia of meso- and metathoracic legs black, remainder of legs salmon pink.

**Male genitalia** (Fig. 6). The interpretation of male genitalia was based primarily on Sibatani et al. (1954). Basal part of valve, composed of dorso-proximal costa and ventro-proximal sacculus, well developed. Heavily sclerotized costa forms right angle at junction of its dorso-proximal and proximal margins. Valvula, ventroapical region of valve beyond membranous annelifer, narrower than basal part of valve, but of equal length. Valvula gradually tapers to simple narrowly rounded apex and lacking digitus. Relatively short harpe curved to form open half circle with its opening facing ventro-apically and inner diameter of 0.5 mm. Transtilla curved with its smaller diameter on its mesal surface. Vincula beyond ventral edge of sacculus form V-shaped structure with length longer than width. Two vincula meet at acute angle. Juxta ends in two heavily sclerotized points forming shallow V, with depth of V equal to half width of juxta at level of base of V. Uncus terminates in widened tip with slight bifurcation. Male genitalia is bilaterally asymmetrical, with apical portion of left valvula being broader than right.





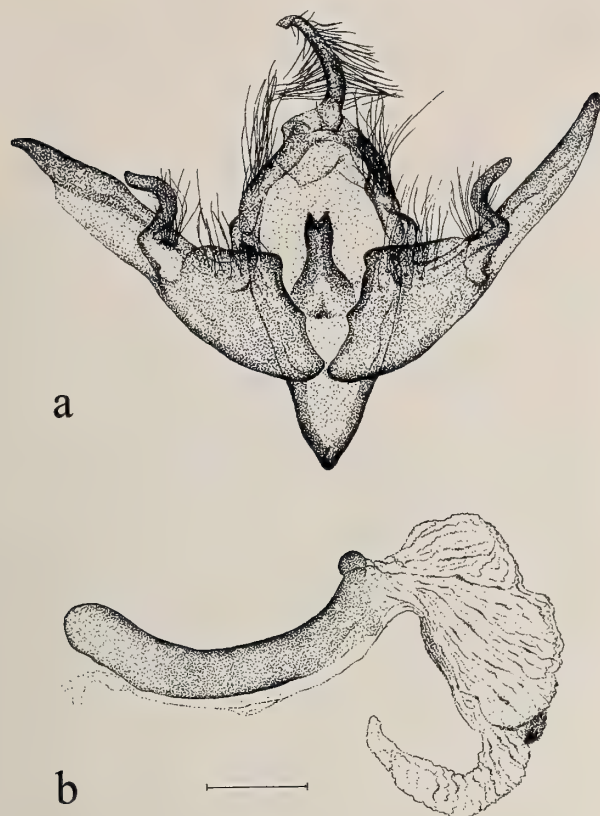


FIG. 6. Male genitalia of *Lithophane thujae*. **a**, Genitalia with aedeagus removed; **b**, Aedeagus. A.W.T. Genitalia vial 95.x.30-#26. Paratype, New Brunswick, York Co., ecl. 22 September 1992, R. P. Webster. Scale bar = 1 mm.

**Female genitalia** (Fig. 7). Similar to, but smaller than *L. lemmeri* (Fig. 8c). Major structural difference is in ventral edge of ostium. In *L. thujae*, sterigma is non-sclerotized and forms a straight, horizontal, edge. It is totally overshadowed by heavily sclerotized lamella antevaginalis which is deeply invaginated giving ostium an apparent V-shaped opening. In *L. lemmeri*, sterigma is distinct, sclerotized, and has wavy edge.

**Diagnosis.** The forewing pattern of *L. thujae* (Figs. 1 and 2) is similar to that of *L. lemmeri* (Figs. 3 and 4), but the markings are bolder and more completely developed in *L. thujae*. In *L. lemmeri*, the wings are a uniform dirty brownish gray, the black median streak between the antemedial and postmedial lines is poorly developed, and the subreniform line is less developed and not outlined anteriorly with white. Rubbed specimens may be mis-identified as *L. lemmeri*, but the forewing patterns of fresh specimens of the two species are distinctively different (Figs. 1-4). *L. lemmeri* has longer narrower wings: forewing length 20.0-20.5 mm, width 7.0 mm ( $n = 4$ ). The male genitalia of *L. thujae* and *lemmeri* are also substantially different (Figs. 6 and 8). In *L. lemmeri* (Fig. 8a), valvula has an expanded costal bulge towards its apex to form a rounded protuber-

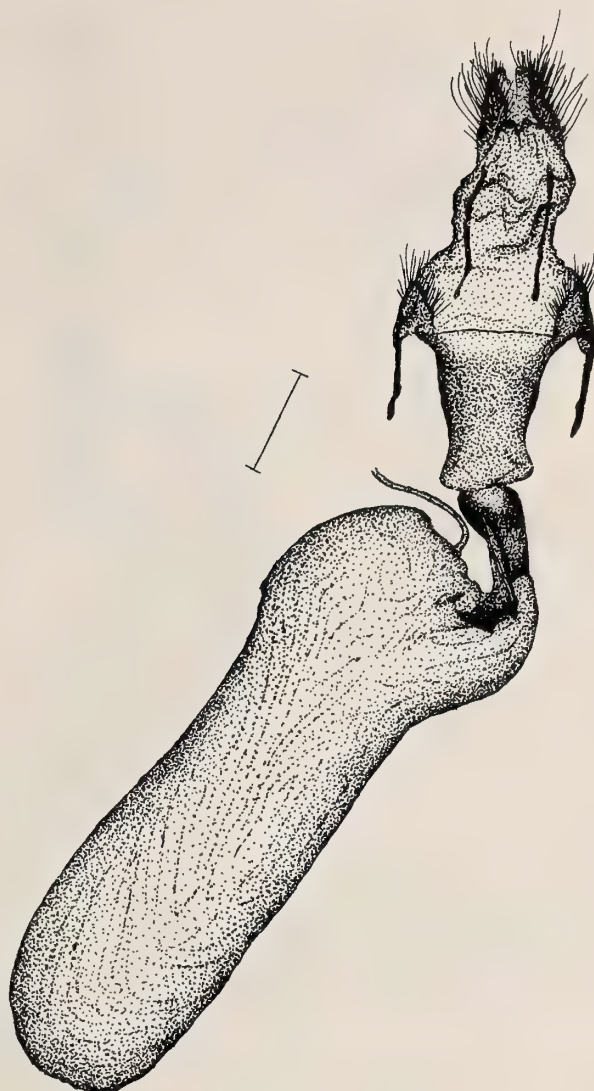


FIG. 7. Female genitalia of *Lithophane thujae*. A.W.T. genitalia vial 95.x.30-#25. Paratype, New Brunswick, York Co., ecl. 19 September 1992, R. P. Webster. Scale bar = 1 mm.

ance on its mesal surface and then narrows to form a distinctively bifurcate tip, with the dorsal branch twice as long as the ventral branch (digitus). In *L. thujae* the valvula (Fig. 6a) lacks a costal bulge and gradually tapers to a simple narrowly rounded tip, without a digitus.

**Types.** *Holotype* male (Fig. 1): CANADA, NEW BRUNSWICK, York Co., 5.3 km SW of Jct. of Hwy. 101 and Charters Settlement Rd. (45°50'38"N, 66°44'31"W), *ex ovum* from female collected at M.V. light 1 June 1992, reared on *T. occidentalis*, emerged 24 September 1992, R. P. Webster. *Allotype* female (Fig. 2): same locality and data as male, emerged 16 September 1992. Paratypes:

FIGS. 1-5. Adults of *Lithophane thujae*, new species and *Lithophane lemmeri*; and larva of *L. thujae*. **1**, *Lithophane thujae*, holotype male. **2**, *Lithophane thujae*, allotype female. **3**, *Lithophane lemmeri*, male, New Jersey, Atlantic Co., Egg Harbor Twp., *ex ovum* 2 April 1994, reared on *Juniperus virginiana*, ecl. 1-4 Nov. 1994, Dale F. Schweitzer. **4**, *Lithophane lemmeri*, female, same data as male. **5**, Mature larva of *Lithophane thujae* on *Thuja occidentalis*. Length 30 mm. Reared *ex ovum* from a female collected at M.V. light on 3 May 1996 at New Brunswick, York Co., R. P. Webster.



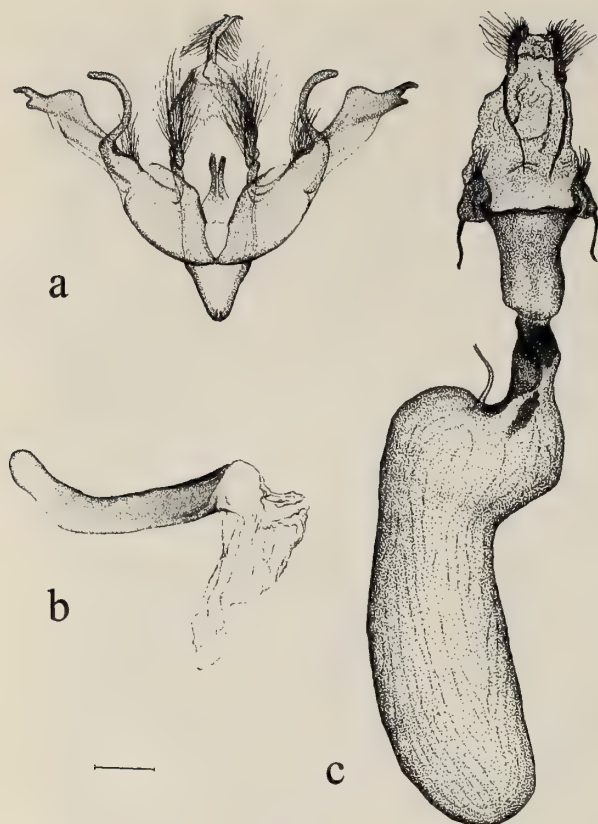


FIG. 8. Male and female genitalia of *Lithophane lemmeri*. **a**, Male genitalia with aedeagus removed; **b**, Aedeagus. A.W.T. genitalia vial 95.x.30-#23. New Jersey, Atlantic Co., Egg Harbor Twp., *ex ovum* 2 April 1994, reared on *Juniperus virginiana*, ecl. 1-4 Nov. 1994, Dale Schweitzer; **c**, Female genitalia. A.W.T. genitalia vial 95.x.30-#24. Same data as male. Scale bar = 1mm.

27 males and 47 females as follows: CANADA, NEW BRUNSWICK: York Co., 3.5 km. S. of Jct. Hwy 3 & 4, Jct. Hwy 3 & Davis Brook, 27 April 1990 (1 female), A. W. Thomas & R. P. Webster; same locality and data as Holotype, emergence dates 16-30 September 1992 (8 males, 14 females), R. P. Webster (2 males and 1 female dissected, A. W. Thomas genitalia vials 95.x.30-#21 (male), 95.x.30-#26 (male), 95.x.30-#25 (female)); same locality as Holotype, 8 October 1994, at M.V. light (1 female), R. P. Webster; same locality as Holotype, *ex ovum* from female collected at M.V. light 3 May 1996, reared on *T. occidentalis*, emergence dates 4-17 September 1996 (17 males, 29 females), R. P. Webster; same locality as Holotype, 13 October 1996, at M.V. light (1 female), R. P. Webster. U.S.A., MICHIGAN: Otsego Co., T29N R2W Section 15, 27 April 1974 (1 male), 13 May 1994 (1 male), both M. C. Nielsen. WISCONSIN: Florence Co., T38N R19E Section 10, 11 October 1980 at light (1 female), J. C. Parkinson.

**Disposition of types.** Holotype (no. CNC-22575) and allotype in the Canadian National Collection, Ottawa, Ontario; paratypes at the American Museum of Natural History, New York; Canadian National Collection, Ottawa, Ontario; Florida State Collection of Arthropods, Gainesville, Florida; National Museum of Natural History, Washington, D.C.; Los Angeles County Museum of Natural History, Los Angeles, California; The Natural History Museum, London, England; Insect Reference Collection, Natural Resources Canada, Canadian Forest Service - Atlantic Forestry Centre, Fredericton, New Brunswick; and private collections of Henry H.

Hensel, Edmunston, New Brunswick; Mogens C. Nielsen, Lansing, Michigan; James C. Parkinson, Mosinee, Wisconsin; Dale F. Schweitzer, Port Norris, New Jersey; Anthony W. Thomas, Fredericton, New Brunswick; Jim Troubridge, Agassiz, British Columbia; Martin N. Turgeon, St. Basile, New Brunswick; Reginald P. Webster, Charters Settlement, New Brunswick.

**Type locality.** The type locality is within a small, partially wooded, residential area 5.3 km SW of the Jct. of Hwy. 101 and Charters Settlement Rd, about 8 km SW of Fredericton, New Brunswick, Canada. The forested area where the *L. thujae* specimens were collected is a mature second growth mixed conifer forest with a small brook passing through it. Dominant species of trees are *T. occidentalis*, *Abies balsamea* (L.) Mill. with scattered *Salix* sp., *Betula allegheniensis* Britt., *B. papyrifera* Marsh., *Acer rubrum* L., and *Fraxinus americana* L. *T. occidentalis* is most abundant near the shaded stream. Openings along the stream are dominated by *Alnus incana* (L.) Moench.

**Etymology.** The specific epithet *thujae* is named after the name of the genus of the probable host plant of this species.

**Biology.** *Lithophane thujae* was reared on *T. occidentalis* on two occasions. In the initial attempt to rear this species, the larvae were offered 21 species of woody plants from the general area where the adults were collected. The larvae accepted only *T. occidentalis* and completed development on this host. *T. occidentalis* is common at the type locality where most specimens of this species have been collected to date and is present at all other known sites for this species and thus, we feel that *T. occidentalis* is the likely host plant for this species. The related *L. lemmeri* also feeds on a member of the Cupressaceae (*Juniperus virginiana* L.) (Dale F. Schweitzer, pers. comm.).

*Lithophane thujae* has five larval instars. A mature last instar of *L. thujae* is shown in figure 5. The mature larvae are 33.0 to 35.0 mm in length and range in color from green to dark green with a series of longitudinal rows of white spots as shown in the figure. This pattern makes the larvae very difficult to locate on the foliage of their host plant. The second through fourth instar caterpillars exhibit a similar color pattern.

A female collected on May 3, 1996, and confined to a 2-liter plastic container laid yellowish white eggs (0.89 mm diam., 0.69 mm high) near the tips of the underside of the foliage of *T. occidentalis*. The description that follows is based on observations of larvae maintained on cuttings of *T. occidentalis* between 12° and 18°C. The eggs hatched 12-15 days after they were laid. The tan-colored first instar larvae gradually turned to light green as they fed near the tips of the new growth. The molt to second instar took place about six days later. The second instar larvae developed the color pattern that persisted through the last instar. The duration of the second, third, and fourth instars was each about six days under this temperature regime. The duration of the last instar was nine to eleven days. All larval instars fed near the tips of the new growth and usually consumed between 1 and 2 mm of the tip of the needle before moving to an adjacent needle. Last instar larvae also fed on the previous year's growth. When development was completed (mid June to early July) the last instar larvae formed cocoons in the leaf litter. However, the larvae did not pupate until late August. Adults emerged in mid September under laboratory conditions.

**Flight season.** *Lithophane thujae* has been collected in October (3 freshly emerged specimens) and during April, May, and early June. Specimens collected in the spring were worn suggesting that *L. thujae*, like other *Lithophane* species, overwinter as adults and will be present in the fall and the following spring.

**Geographical distribution.** South central New Brunswick, northern Michigan and northern Wisconsin. Probably has a broader distribution and will likely be found in intervening areas where *T. occidentalis* is common.

## DISCUSSION

*Lithophane thujae* is a member of an assemblage of *Lithophane* species which feed during the larval stage

on members of the Cupressaceae. These species include *L. lemmeri* from the Atlantic coastal plain of the U.S.A. from Connecticut southward (Dale F. Schweitzer, pers. comm.); *L. subtilis* Franclemont, *L. tarda* (Barnes and Benjamin), and *L. longior* (Smith) from southwestern North America (Franclemont 1969); and the Palearctic *L. leautieri* Boursin (Bretherton et al. 1983). None of these species has a combination of wing pattern and male genitalia similar to *L. thujae* (Barnes and Benjamin 1929, Boursin 1971, Bretherton et al. 1983, Franclemont 1969). Although the wing pattern of the more northern *L. thujae* and *L. lemmeri* are similar, the genitalia of the two are very different.

Very few field-collected specimens are currently known of *L. thujae*. The reason for this apparent rarity is unclear. Possibly *L. thujae* is less attracted to light or bait than other *Lithophane* species, or has very specific habitat requirements. The current distribution includes only New Brunswick, Michigan, and Wisconsin. However, it is likely that this species will be found in the intervening areas in Maine, northern New Hampshire, Quebec and Ontario once more collecting is done in habitats with *T. occidentalis*.

#### ACKNOWLEDGMENTS

Many thanks are due to Dale Schweitzer, Port Norris, New Jersey, for sharing unpublished data on the biology of *L. lemmeri*, sup-

plying specimens of *L. lemmeri*, and providing invaluable information on the location of specimens of *L. thujae* in eastern North American institutional and private collections obtained during a survey of the distributional records of *L. lemmeri*. We thank Donald Lafontaine, Biosystematics Laboratory, Ottawa, Canada, for supplying information on the location of possible *L. thujae* specimens in The Canadian National Collection and other Canadian institutions. We thank Martin Honey for supplying information on *L. leautieri* and the location of possible *L. thujae* in The Natural History Museum, London, England. We thank Mogens C. Nielsen, Lansing, Michigan, and James C. Parkinson, Mosinee, Wisconsin, for loaning specimens of *L. thujae*. We thank P. Z. Goldstein and two anonymous reviewers for helpful suggestions on the manuscript.

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## A NEW GENUS OF TORTRICID MOTHS (TORTRICIDAE: EULIINI) INJURIOUS TO GRAPES AND STONE FRUITS IN CHILE

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**ABSTRACT:** *Accuminulia*, new genus, is described and illustrated from Chile. The new genus includes two species: *A. buscki*, new species (type species), and *A. longiphallus*, new species. *Accuminulia buscki* has been reared from the fruit of grape (*Vitis* sp.; Vitaceae), plum (*Prunus domestica*; Rosaceae), apricot (*Prunus armeniaca*; Rosaceae), and peach (*Prunus persica*; Rosaceae) in Chile; the oldest specimen examined is an adult intercepted at the port of New York in cargo (grapes) from Chile in 1926. Several specimens of *A. buscki* have been collected recently (1983) in traps baited with *Proeulia*-lure. The new genus is assigned to Euliini on the basis of its putative phylogenetic relationship to *Proeulia* Clarke.

**Additional key words:** pest species, Neotropical, Euliini, systematics, *Vitis*, *Prunus*.

In 1926 an adult of an undescribed tortricid moth was intercepted at the port of New York in cargo (grapes) that originated from Chile. The late August Busck, a lepidopterist at the National Museum of Natural History, recognized the moth as representing a new genus and species, but did not describe it, probably owing to the lack of sufficient material. Over the 70 years since that interception, numerous specimens of the species have accumulated—both sexes, the pupa, and larval food plants now are known. A second undescribed congener also is known from Chile. This paper describes and illustrates the new genus and its two species, and presents information on the biology of one of them.

### MATERIALS AND METHODS

Taxonomic material was obtained from the following institutions: The Natural History Museum (BMNH), London, England; Mississippi Entomological Museum (MEM), Mississippi State, Mississippi, U.S.A.; Essig Museum of Entomology, University of California, Berkeley (UCB), California, U.S.A.; and National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., U.S.A. Dissection methodology follows that summarized in Brown & Powell (1991). Illustrations of genitalia and wing venation were drawn with the aid of a Ken-A-Vision microprojector (model X1000-1). Forewing measurements were made with an ocular micrometer mounted in a Leica MZ12 dissecting microscope. Terminology for wing venation and genitalic structures follows Horak (1984). Abbreviations and symbols are as follows: FW = forewing; HW = hindwing; DC = discal cell; n = number of specimens examined;  $\bar{x}$  = mean; ca. = circa (approximately).

### SYSTEMATICS

#### *Accuminulia* J. Brown, new genus

**Type species.**—*Accuminulia buscki* J. Brown, new species.

**Description. Adult.** *Head:* Antennal cilia ca. 0.5–0.8 times flagellomere diameter in male, ca. 0.1 times flagellomere diameter in female. Labial palpus (all segments combined) ca. 1.5 times horizontal diameter of compound eye, segment II weakly upturned, slightly expanded distally by scaling, segment III 0.2–0.3 times as long as II, smooth-scaled, exposed. Maxillary palpus rudimentary. Dorsal portion of frons with short overhanging tuft of scales. Ocelli present. Chaetosema present. Proboscis ca. as long as segment II of labial palpus, presumably functional. *Thorax:* Smooth-scaled. Legs unmodified, male foreleg without hairpencil. *Forewing* (Fig. 1): Length ca. 1.8 times width; length of DC ca. 0.68 times FW length; width of DC ca. 0.18 times DC length;  $CuA_2$  originates ca. 0.70 along length of DC; all veins separate beyond DC; chorda weak but present; M-stem absent; CuP absent. Upraised scale tufts present (*A. longiphallus*) or absent (*A. buscki*); male without costal fold. *Hindwing:* Sc+R and Rs approximate; Rs to costa before apex; Rs and  $M_1$  stalked ca. 0.4 distance;  $M_2$  and  $M_3$  approximate;  $M_3$  and  $CuA$  stalked ca. 0.3 distance; CuP present; M-stem absent; tuft of hairlike scales along 1A+2A (cubital pecten), originating near base of wing; male with (*A. longiphallus*) or without (*A. buscki*) modified sex scaling on basal portion of wing. *Abdomen:* Dorsal pits absent; no modified corethrogynae scaling in female. *Male genitalia* (Figs. 2–3): Uncus simple, rodlike, weakly curved. Socius moderate in size, ca. 0.7 length of gnathos arms, pendant, rounded; not fused to gnathos. Gnathos complete, arms narrow, joined distally into expanded triangular plate with densely spined venter. Subscaphium and hami absent. Transtilla a moderately broad, arched plate, with a sclerotized posterior band bearing a dense row of short, fine, spinelike teeth. Valva moderately slender, parallel-sided, rounded apically; sacculus simple, well defined at base, without free apical process(es); costa weakly differentiated. Pulvinus absent. Vinculum complete, well developed. Juxta a sclerotized subrectangular plate with lateral pointed processes at dorsum. Aedeagus broad, moderately short, with sclerotized, attenuate, thornlike process distally; phallobase simple, rounded; vesica with variable number of mostly lanceolate cornuti. *Female genitalia* (Figs. 4–5): Papillae anales slender. Apophyses anteriores and posteriores long, slender, posteriores slightly longer. Sterigma a slender, weakly sclerotized band. Antrum large, broad, membranous, with slender, sclerotized dorsal band; accessory pouch weakly developed on right side, either as a slightly expanded area with an irregular line of sclerotization or as a triangular flap. Ductus bursae broad, moderately long, with longitudinal creases of sclerotization, twisted about two-thirds distance from antrum to junction with corpus. Corpus bursae rounded, finely punctate; signum lacking.

**Pupa** (Figs. 6–7). Description and illustrations based on reconstructions of 3 pupal shells (i.e., adults eclosed) of *A. buscki*. Typically tortricine; head without apical projection; no conspicuous sculpturing on dorsum of T3 or A1–2 (similar to *Anopina* Obraztsov and *Chileulia* Powell, and in contrast to *Dorithia* Powell and *Cuproxena* Powell & Brown); abdomen with two rows of spines dorsally on A2–7, one row on A8–9; rows on A2 well developed in con-



FIG. 1. Wing venation of *Accuminulia buscki*.

trast to that of other euliine pupae examined; cremaster short and broad, with 4 pairs of long, hooked setae. The pupa of *Accuminulia* differs from that of *Dorithia* and *Cuproxena* (both Euliini) in the following: 1) absence of ornate sculpturing on the dorsum of abdominal segments T3 and A1–2 (see Brown & Powell 1991 for comparison); 2) the anterior row of spines on the dorsum of segments A3–7 extends from spiracle to spiracle across the dorsum (in *Dorithia* and *Cuproxena* the row is restricted to approximately the middle 0.6 of the dorsum); and 3) the cremaster is short and broad compared with that of *Dorithia* and *Cuproxena*.

**Diagnosis.** Superficially, adults of *Accuminulia* are similar to *Apotomops* Powell and *Bonagota* Razowski on the basis of size and pattern of the forewing, size and shape of the labial palpus, and length of the antennal cilia. However, the only feature of the genitalia reminiscent of those two genera is the weakly developed accessory pouch in the female; a well defined accessory pouch is one of several convincing synapomorphies demonstrating the sister relationship of *Apotomops* and *Bonagota* (Brown & Powell 1991). The male genitalia of *Accuminulia* are similar to those of *Varifula* Razowski in the possession of a thornlike sclerite at the distal end of the aedeagus and a densely spined transtilla. In contrast, the facies of *Accuminulia* are remarkably dissimilar to those of *Varifula*: forewing length in *Varifula* varies from 12–15 mm, that of *Accuminulia* from 6–7 mm; forewing color and pattern in *Varifula* are simple with mostly yellow and pale tan, those of *Accuminulia* are complex, mottled gray, black, and white; and the labial palpi are extremely elongate (ca. 2.2 times compound eye diameter) and nearly porrect in *Varifula*, while short (ca. 1.5 times compound eye diameter) and weakly upturned in *Accuminulia*. Autapomorphies for *Accuminulia* include the enlarged, triangular, ventrally spined distal portion of the gnathos, the narrow, parallel-sided valvae, and the partially twisted ductus bursa.

Although documented food plants of *Accuminulia* are similar to those of *Chileulia stalactitis* (Meyrick), a Chilean species also known to feed on grapes and various *Prunus* species (see Powell 1986, Brown & Passoa 1998), the two genera have little in common morphologically.

**Etymology.** The generic name is a combination of parts of three words: “accumulate,” “in,” and “Eulia” Hübner; it is interpreted as masculine in gender.

**Phylogenetic relationships.** Based on the large, broad aedeagus with long, strong cornuti in the male and corresponding large, variably sclerotized antrum and ductus bursae of the female, *Accuminulia* appears to belong to a group of genera that includes *Proeulia*

Clarke, *Argentulia* Brown, *Varifula*, *Inape* Razowski, and *Subtranstillaspis* Razowski. *Accuminulia* shares with *Argentulia*, *Varifula*, and several species of *Proeulia* a slender, sclerotized, attenuate process along the lateral margin of the distal portion of the aedeagus. It shares with *Varifula* an extremely similar, densely spined transtilla (see Razowski 1995 for comparison). Although the spined transtilla appears to represent a convincing synapomorphy for *Accuminulia* and *Varifula*, their considerable phenotypic difference, their dissimilar cornuti, and their extremely dissimilar female genitalia shed doubt on their possible sister group relationship. Superficially, *Varifula* looks like *Proeulia*, and its female genitalia are extremely similar to those of *Argentulia*.

The assignment of *Accuminulia* to the tortricid tribe Euliini is based on the hypothesized phylogenetic relationship with *Proeulia*, which possesses the characteristic euliine foreleg hairpencil in the male (Brown 1990). The presence of a gnathos excludes it from Cochylini, which it resembles superficially and in the possession of an extremely broad aedeagus.

#### KEY TO MALES OF ACCUMINULIA

1. Hindwing without modified sex scales in basal one-half, mostly dingy white with pale gray mottling (Fig. 8) . . . . . *buscki*
- 1'. Hindwing with basal one-half covered by modified sex scales, cream-white in contrast to pale gray-brown of remainder of hindwing (Fig. 10) . . . . . *longiphallus*

#### *Accuminulia buscki* J. Brown, new species

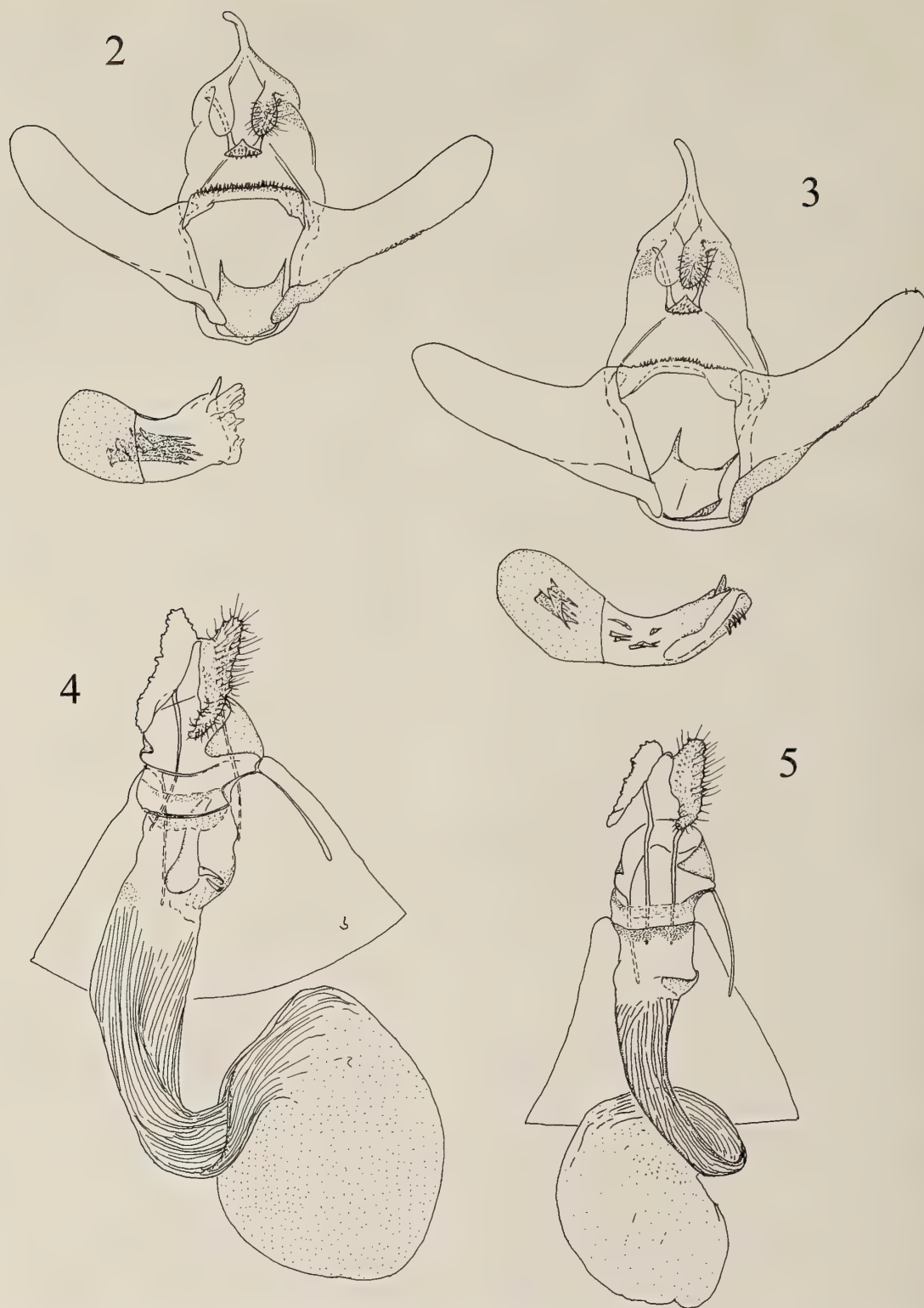
Figs. 1, 2, 5–9

**Description. Male.** *Head:* Frons smooth-scaled below mid-eye, whitish; roughened above, red-brown, pale yellow, and white. Labial palpus whitish yellow and brown mesally; brown mixed with tan laterally. Antennal scaling pale tan. *Thorax:* White, with brown and tan at anterior portion. *Forewing* (Fig. 8): Length 6.5–8.0 mm ( $\bar{x}$  = 6.9 mm;  $n$  = 8). Upper side whitish tan, with irregular gray, brown, and cream overscaling and irrorations; gray rhomboidal or semicircular patches at costa ca. 0.3 and 0.5 distance from base to apex; ill defined, transverse, reddish brown band in distal 0.33, bordered basally by a white band; white band well defined at dorsum, becoming less defined toward costa; small black spot at apex of DC. Under side uniform dark tan with faint indication of upperside markings. *Hindwing:* Upper side dingy white, with pale gray overscaling and mottling. Under side light gray-brown with darker mottling. *Abdomen:* Light cream. *Genitalia:* As in Fig. 2 (drawn from USNM slide 88447;  $n$  = 8). Uncus, socius, gnathos, transtilla, and valva as described for the genus. Aedeagus extremely short, broad, with 5–6 large, narrow-triangular cornuti, with broad bases.

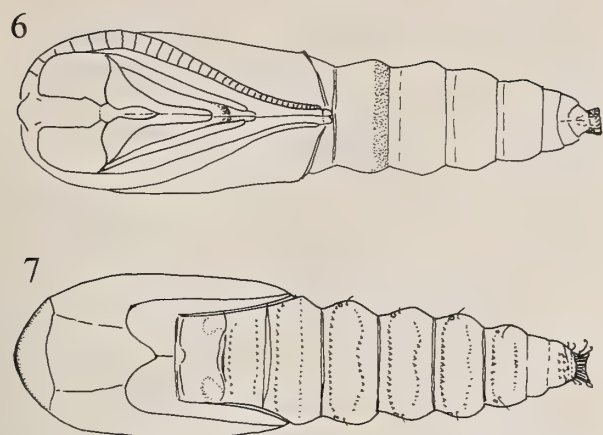
**Female.** FW length 6.0–7.0 mm ( $\bar{x}$  = 6.6 mm;  $n$  = 5). Superficially as in male (Fig. 9), except forewing with basal 0.5 mostly whitish with grayish overscaling, pattern slightly more defined; antennal cilia shorter. *Genitalia:* As in Fig. 5 (drawn from USNM slide 68618;  $n$  = 3). Essentially as described for the genus.

**Holotype.** ♂, Chile, Santiago Province, 29 Mar 1954, reared from grape (fruit), emerged 12 Apr 1954, 54-3351 (M. J. Ramsay, USNM).





FIGS. 2-5. Genitalia of *Accuminulia*; males with valvae spread, aedeagus removed. 2. Male of *A. buscki*; 3. Male of *A. longiphallus*; 4. Female of *A. longiphallus*; 5. Female of *A. buscki*.



FIGS. 6–7. Pupa of *Accuminulia buscki*. 6. Ventral aspect; 7. Dorsal aspect.

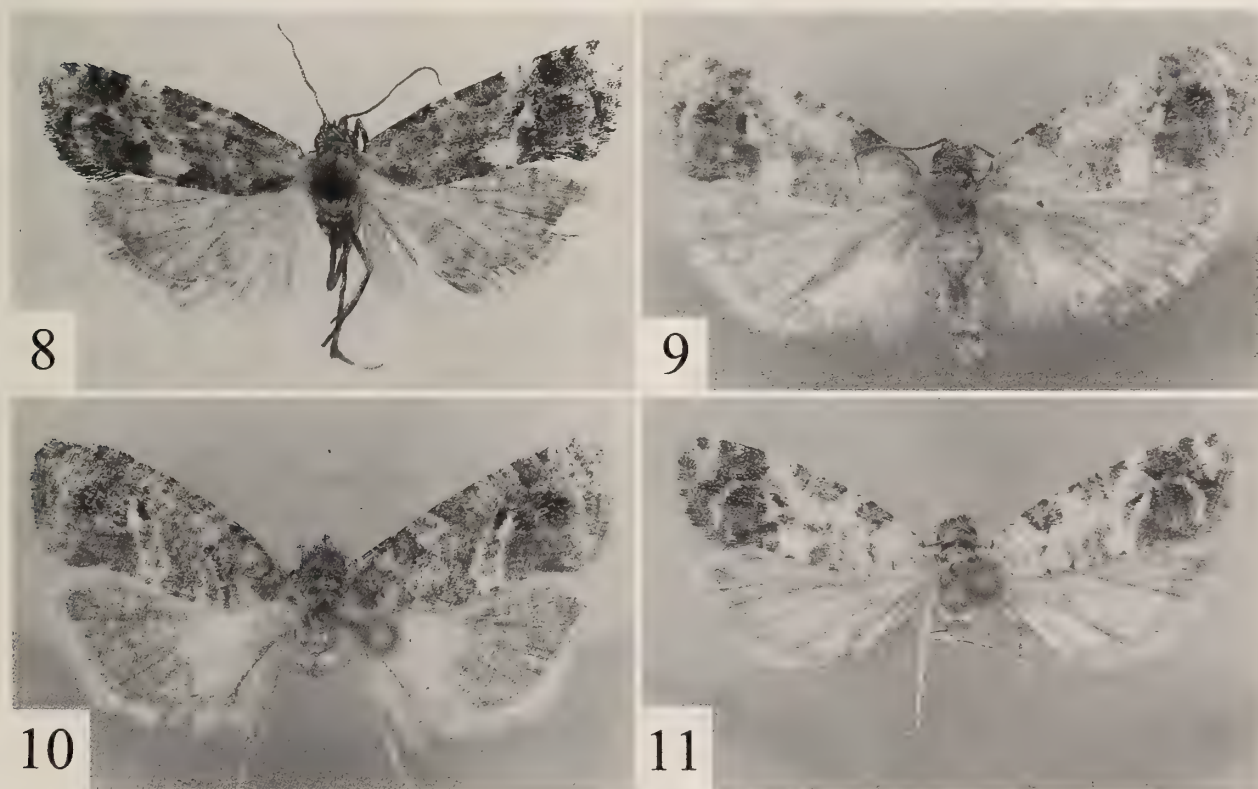
**Paratypes.** 10 ♂♂, 17 ♀♀ as follows: CHILE: *Aconcagua Province*: Los Molles, ca. 10 km S Pichidangui, 1 ♀, 15/17 Nov 1981 (D. & M. Davis, USNM). *Coquimbo Province*: Fray Jorge National Park, ca. 70 km W Ovalle, 1 ♀, 6/9 Nov 1981 (D. & M. Davis, USNM); Nague, 11 km N Los Vilos, 20 m, 1 ♀, 4/5 Nov 1981 (D. & M. Davis, USNM); Cta. Cavilolen, NE Los Vilos, 5 ♀♀, 5 Feb 1986 (L. Peña, USNM); El Naranjo, S Caimanes, 1 ♀, 7 Feb 1986 (L. Peña, USNM); La Viluma, SE Melipilla, 350 m, 1 ♀, 15/17 Dec 1987 (L. Peña, USNM); Coquimbo, 1 ♂, 12 Mar/14 May 1884 (Walker 3214, BMNH). *Ñuble Province*: Alto Tresgualemu, ca. 20 km SE Chovellen, 1 ♀, 1/3 Dec

1981 (D. & M. Davis, USNM). *Santiago Province*: Santiago, 1 ♀, 5 Apr 1954, reared from grapes, 4-3161 (M. J. Ramsay, USNM), 1 ♀, 5 Apr 1954, reared from peach, 54-3165 (F. Rotundo, USNM), 1 ♀, 24 Feb 1954, reared from peach, 54-2979 (M. J. Ramsay, USNM), 1 ♀, 9 Feb 1954, reared from peach, 54-2233 (Damos, USNM), 1 ♀, 22 Mar 1954, emerged 2 Apr 1954, reared from plum (fruits), 54-3352 (M. J. Ramsay, USNM), 1 ♂, Nov 1955, reared from apricot fruit (G. Olalquiaga, USNM), 1 ♂, 17 Feb 1954, reared from peach (M. Ramsay, USNM); Santiago, ex-*Proeulia* bait, 1 ♂, 5 Sep 1983 (P. Alvarez, UCB), 2 ♂♂, 3 Sep 1993 (R. Gonzales, UCB), 1 ♂, Sep 1993 (D. Cepeda, UCB), 1 ♂, 8/12 Nov 1993 (R. Gonzales, UCB); Río Colorado, ca. 40 km SE Santiago, 1100 m, 1 ♀, 29/31 Oct 1981 (D. & M. Davis, USNM); Valparaiso, 1 ♂, 30 Sep/8 Oct 1883 (Walker 3070, BMNH). USA: *New York*: In cargo [packaged grapes] from Chile, on ship, 1 ♂, NY #57651, A. Busck gen. prep. 22 May 1926 (USNM).

**Remarks.** In the female paratype reared from grapes, the accessory pouch is considerably more developed, represented by a conspicuous triangular flap lacking sclerotization. Although it is possible that this specimen is not conspecific with the remaining series, its conformity in phenotype and all other morphological features to other specimens, in addition to its food plant, suggest that the unusual pouch represents infraspecific variation.

**Etymology.** This species is named in honor of the late August Busck, one of the most prolific early microlepidopterists at the U.S. National Museum of Natural History.

**Distribution and biology.** *Accuminulia buscki* is known only from Chile; captures range from 20 to 1100 m elevation. Specimen records suggest an adult flight period from October through April. It has been reared from the fruit of grape (*Vitis* sp.; Vitaceae),



FIGS. 8–11. Adults of *Accuminulia*. 8. *A. buscki* (male); 9. *A. buscki* (female); 10. *A. longiphallus* (male); 11. *A. longiphallus* (female).



plum (*Prunus domestica* L.; Rosaceae), apricot (*Prunus armeniaca* L.; Rosaceae), and peach (*Prunus persica* (L.) Batsch; Rosaceae). Captures in native habitat suggest that it is not an introduced pest in Chile, but a native species that has expanded its food plant range to include exotic (i.e., agricultural) plants. Although most larval Tortricinae are leaf-rollers, a few genera are known to bore into the fruit of their food plants. In Euliini these include *Proeulia* Obraztsov, *Chileulia* Powell, and *Accuminulia*, all from Chile (see Brown & Passoa 1998).

*Accuminulia buscki* was first recorded as an interception at the port of New York in cargo (grapes) from Chile. Nearly all current interceptions of Lepidoptera at United States ports of entry are larvae. Because the larva of *Accuminulia* remains unknown, it is impossible to determine whether this species currently is intercepted in fruit from Chile. Because grapes from Chile routinely are fumigated at U.S. port of entry, foliage-feeding insects are eliminated (J. Cavey pers. comm.). However, larvae feeding within fruit may be unaffected by such treatments.

Recent collections (1983) of this species have come from traps baited with *Proeulia*-lure. Several species of *Proeulia* are pests of crops in Chile, including grapes, citrus, kiwis, and various stone fruits.

### *Accuminulia longiphallus* J. Brown, new species Figs. 3–4, 10–11

**Description. Male.** *Head:* Frons smooth-scaled below mid-eye, white mixed with red-brown; roughened above, dark gray-brown. Labial palpus white and gray mesally; mostly brown laterally. Antennal scaling red-brown on scape, whitish on flagellomeres. *Thorax:* Mixed white, red-brown, and tan. *Forewing* (Fig. 10): Length 6.5–7.8 mm ( $\bar{x}$  = 7.2 mm;  $n$  = 2). Upper side mostly gray, with irregular tan, black, and cream overscaling and irrorations; distal 0.25 with moderately dense red-brown overscaling; patch of upraised cream scales at dorsum near base; an irregular, lustrous white band from near middle of dorsum, terminating just basad of apex of DC; diffuse black patch of overscaling distad of termination of white line. Under side uniform dark tan with faint indication of upperside markings. *Hindwing:* Upper side with basal 0.5 covered by modified sex scaling, cream-white; patch of sex scales just below costa near base; distal 0.5 of wing pale gray-brown. Under side light gray-brown with darker mottling. *Abdomen:* Light cream. *Genitalia:* As in Fig. 3 (drawn from RLB slide 1087;  $n$  = 2). Uncus, socius, gnathos, transtilla, and valva as described for the genus. Aedeagus comparatively long, curved in distal 0.4, with a patch of 4 short, external teeth near tip; 10–12 short, spinelike cornuti in vesica.

**Female.** FW length 6.1 mm ( $n$  = 1). Superficially as in male (Fig. 11), except forewing mostly whitish in basal 0.5; antennal cilia shorter. *Genitalia:* As in Fig. 4 (drawn from RLB slide 1085;  $n$  = 1). As described for the genus, except accessory pouch poorly defined, represented by a pair of spinelike sclerites (possibly deciduous cornuti?).

**Holotype.** ♂, Chile, Santiago Province, 6 km W Tiltit, 15 Dec 1982 (R. L. Brown, MEM).

**Paratypes.** 1♂, 1♀ as follows: CHILE: 1♂, same data as holotype. Aconcagua Province: 10 km E San Felipe, 1♀, 14 Dec 1982 (R. L. Brown, MEM).

**Etymology.** The specific epithet refers to the comparatively long aedeagus of this species.

**Distribution and biology.** *Accuminulia longiphallus* is known only from Chile. It has been recorded only from Santiago and Aconcagua, provinces in which *A. buscki* also has been collected. Nothing is known of the biology; the three adults were collected in December.

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## PRELIMINARY ESTIMATES OF LEPIDOPTERA DIVERSITY FROM SPECIFIC SITES IN THE NEOTROPICS USING COMPLEMENTARITY AND SPECIES RICHNESS ESTIMATORS

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**ABSTRACT.** Lepidoptera were collected and species richness and complementarity or uniqueness were compared between two rainforest sites: Pakitza, Peru and Beni, Bolivia. The total number of species collected from both sites was 1,879 of which 60 were shared resulting in a complementarity of 96.8%. Non-parametric equations and species accumulation curves of *Hemiceras* Guenée (Lepidoptera: Notodontidae) were used to compare species richness between three rainforest sites, Pakitza and Tambopata, Peru and Reserva Étnica Waorani, Onkone Care, Ecuador. Cluster analysis, using complementarity values for selected sites was used to determine altitudinal relationships between sites in Costa Rica; relationships between forest types in Brazil; and faunal differences among sites in western Amazonia using *Hemiceras*.

**Additional key words:** Biodiversity, Notodontidae, *Hemiceras*, Chao, jackknife.

Biodiversity as defined by E. O. Wilson (Reaka-Kudla et al. 1997) is "everything". Biodiversity encompasses the genes within a single local population or species, the species within a local community, and communities comprising the diverse ecosystems of the world. Life on earth is supported by the interactions and products produced by all other life on earth. Without biodiversity there would be no life on earth as we know it. Therefore, it is essential that biologists begin to document and record biodiversity, whether it be how many species of insects are in your backyard to how many species of trees in a forest to how many forest types in the world.

Anyone with an interest in natural history can begin to study their local biodiversity and to document it. One basic element of biodiversity is to know how many species are present at a particular site. This paper will outline how anyone can begin to document local biodiversity by gathering data on species richness or the number of species present at a site at a particular point in time. Knowing what species are present at a site is essential because it is the first step in understanding the interactions between the species documented and their interactions within the local community and ecosystem.

Presently, no one has much of an idea exactly how many species are present today on earth. Estimates of the number of species worldwide range from 3 to 100 million (Erwin 1982, 1983, Stork 1988, Hodkinson & Casson 1991, May 1992, Raven and Wilson 1992). The study of species richness and complementarity, or how different species composition is between sites, is essential to assessing global biodiversity patterns.

To address the question of world insect diversity one must get accurate estimates of site-specific species richness for a variety of taxa (Colwell & Coddington 1994), and then to compare these species lists to measure relative levels of overlap and richness of these

taxa around the globe. After a site has been sampled, species richness estimates are used to predict how many species were missed during the sampling process, thus arriving at an estimated number of species based on the actual number observed plus the number missed. By using species lists, either generated by sampling at a site or from museum collections, species composition among sites can be compared. These comparisons can then be used in setting policy and making informed conservation and management decisions.

The goals of this paper are 1) to emphasize the importance of adequate sampling, 2) to assess whether inadequate sampling can still be useful in predicting species richness and complementarity between study sites, and 3) to provide a method of using complementarity to compare faunal relationships between sites. To accomplish these goals, I compared overall species richness and complementarity of Lepidoptera from two rainforest sites, one in Peru and the other in Bolivia. In addition, I estimated species richness from species accumulation curves and non-parametric estimators to compare the *Hemiceras* Guenée (Notodontidae) fauna between 2 sites in Peru and 1 in Ecuador. Finally, museum specimens of *Hemiceras* were used for faunal comparisons among sites in Costa Rica, Brazil, and western Amazonia, using complementarity and cluster analysis.

### MATERIALS AND METHODS

**Lepidoptera complementarity in SW Amazonia.** Lepidoptera were collected at two rainforest sites: Beni, Bolivia and Pakitza, Peru. The Beni study site at 14°49' S, 66°28' W is 40 km E of San Borja, at 250 meters elevation. Pakitza is located on the Río Manu at 11°56'47"S, 71°17'00"W within the large drainage basin of the Río Madre de Dios in southeastern Peru, at 356 m elevation, approximately 550 km NW of Beni.



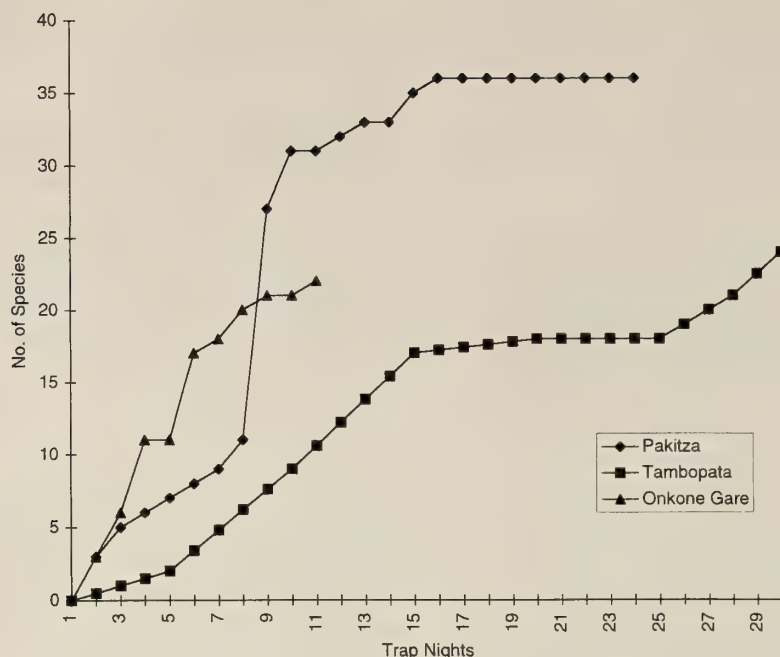


FIG. 1. Species accumulation curves of *Hemiceras* at Pakitza and Tambopata, Perú, and Onkone Gare, Ecuador.

Samples were collected between August 26–September 15, 1987 (Beni) and from September 27–October 5, 1987 (Pakitza). Adult moths were collected by UV light traps, spread, identified to family, sorted to morpho-species, and counted. Voucher specimens have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Collecting effort was defined as the number of trap nights: 12 and 8 trap nights in Pakitza and Beni, respectively. Other studies have included the number of person-hours spent collecting (Coddington et al. 1991, Robbins et al. 1996), number of collecting days (Louton et al. 1996), or trap nights (approximately 12 hours in length).

The Lepidoptera faunas of Pakitza and Beni were compared using complementarity (Colwell and Coddington 1994). In comparing two sites,  $j$  and  $k$ , the first site has a species richness of  $S_j$  and the second site has  $S_k$ . If the number of species in common between both sites is  $V_{jk}$ , then the total species richness for both sites is

$$S_{jk} = S_j + S_k - V_{jk} \quad (1)$$

and the number of species unique to both sites ( $U_{jk}$ ) is

$$U_{jk} = S_j + S_k - 2V_{jk} \quad (2)$$

The complementarity between the two sites is the proportion of the unique species to the pooled richness, or

$$C_{jk} = \frac{U_{jk}}{S_{jk}} \quad (3)$$

***Hemiceras* species richness in western Amazonia.** The genus *Hemiceras* (Lepidoptera: Notodontidae), representing 245 species, was used as an indicator group for estimating species richness at three rainforest sites: Pakitza and Río Tambopata Research Station in southeastern Peru, and Onkone Gare, in Ecuador.

Río Tambopata Research Station, at 14°14'S, 69°11'W, is located on the Río Tambopata, 30 air km SE of Puerto Maldonado, Madre de Dios, Peru, at 290 m elevation. Onkone Gare, at 00°38'S, 76°36'W, is a research station within the Reserva Ethnica Waorani, Ecuador, at 220 m elevation. Tambopata had a total of 29 trap nights from November 2–25, 1979 and September 16–21, 1990. The 11 trap nights at Onkone Gare were January 10, 12, 13–18, 25; June 20; and July 16, 1994.

Species accumulation curves (Fig. 1) were used to plot the cumulative number of new species collected over unit effort (number of trap nights) at each of the



FIG. 2. Localities of Costa Rican sites used in cluster analysis of dissimilarity matrix in Table 3.

FIG. 3. Localities of South American sites used in cluster analyses of dissimilarity matrices in Tables 4 and 5.

three sites. To extrapolate total species richness from the species accumulation curves at each site, four different nonparametric equations were compared: 1) Chao 1, 2) Chao 2, 3) first-order jackknife, and 4) second-order jackknife.

Chao (1984) developed a simple estimator of the true number of species at a given site based on the number of rare species in the pooled sample  $j$ . This is considered an abundance-based estimator because it is based on the number of species that are only represented by only 1 or 2 individuals to estimate overall species richness. Colwell and Coddington (1994) called this Chao 1,

$$\text{Chao 1} = S_{\text{obs}} + a^2/2b, \quad (4)$$

where  $S_{\text{obs}}$  is the observed number of species in a sample,  $a$  is the number of species that are only represented by one specimen in the pooled sample (singletons), and  $b$  is the number of species represented by two specimens in the pooled sample (doubletons). This estimator works well when the samples contain a large number of rare species (Chao 1984), which frequently occurs when sampling diverse groups such as insects.

A related estimator is Chao 2 (Colwell & Coddington 1994), which is based on the incidence of rare species among samples,

$$\text{Chao 2} = S_{\text{obs}} + L^2/2M, \quad (5)$$

where  $L$  is the number of species that occur in only one sample, and  $M$  is the number of species that occur in exactly two samples.

Jackknife estimators (Burnham & Overton 1978, 1979) also use the distribution of species among samples (Colwell & Coddington 1994). The first-order

jackknife estimator of species richness is based on the number of species that occur in only one sample  $L$ ,

$$1 \text{ jackknife} = S_{\text{obs}} + L(n - 1/n), \quad (6)$$

where  $n$  is the number of samples.

The second-order jackknife (Burnham & Overton 1978, 1979) is like the Chao 2 estimator where  $L$  is the number of species that occur in only one sample and  $M$  is the number of species that occur in exactly two samples,

$$2 \text{ jackknife} = S_{\text{obs}} + \frac{1}{2} [L(2n - 3)/n - M(n - 2)^2/n(n - 1)], \quad (7)$$

where  $n$  is the number of samples.

**Hemiceras faunal comparisons between three tropical regions.** Species lists of *Hemiceras* were compiled from specimens in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., and were used to examine faunal relationships among sites in Costa Rica, Brazil, and western Amazonia. In Costa Rica, six sites were chosen to see how altitude affected species composition. The sites chosen were Juan Vinas (1500 m), Tuis (732 m), Turrialba (634 m), Guapiles (259 m), La Selva (40 m) and Sixaola River (0 m) (Fig. 2). Six sites in Brazil were chosen to examine the effect of forest type: the lowland Amazonia forest included the sites of São Paulo de Olivença (Amazonas) and Porto Velho (Rondonia), and the Atlantic coast forest sites were Baixo Guandu (Espírito Santo), Campo Bello (Rio de Janeiro), Hansa Humboldt (Santa Catarina), and Santa Catherines (Santa Catarina) (Fig. 3, sites 1–6). Six sites were chosen to determine faunal relationships in western Amazonia. They included Neblina, Venezuela; Onkone Gare, Ecuador; São Paulo



TABLE 1. Comparison of % complementarity and number of species of Lepidoptera between Beni, Bolivia and Pakitza, Peru.

Family	% Complementarity	Number shared species
Microlepidoptera		
Cosmopterygidae	100.0	50 (0)
Tineidae	100.0	113 (0)
Gelechiidae	98.8	167 (2)
Oecophoridae	97.8	324 (7)
Pyalidae/Crambidae	96.8	281 (9)
Macrolepidoptera		
Noctuidae	98.6	296 (4)
Notodontidae	95.2	63 (3)
Geometridae	93.3	213 (14)
Arctiidae	91.5	189 (16)

de Olivença and Porto Velho in Brazil; and Pakitza and Tambopata in Peru (Fig. 3, sites 1–2, 7–10).

Complementarity was calculated between sites. These values were used to produce dissimilarity matrices which were converted, for easier interpretation, into dendrograms using cluster analysis (SYSTAT 1992).

## RESULTS

### Lepidoptera complementarity in SW Amazonia.

Some 38 families of Lepidoptera were collected from both sites, although only nine families had numbers of species sufficient to illustrate trends in complementarity. Five of these families were Microlepidoptera and the remaining four were Macrolepidoptera. A total of 1748 specimens representing 933 species were collected at Beni and 1731 specimens representing 1006 species from were collected at Pakitza. The pooled species richness for both sites ( $S_{jk}$ ) was 1879, the total number of unique species ( $U_{jk}$ ) was 1819, resulting in a complementarity of 96.8%. The Microlepidoptera families had higher complementarity values (100–96.8%), than the Macrolepidoptera families (95.2–91.5%), with the exception of the Noctuidae (98.6%) (Table 1).

**Hemiceras species richness in western Amazonia.** Comparing the four nonparametric equations for estimating species richness of *Hemiceras* at Pakitza and Tambopata, Peru, and at Onkone Gare, Ecuador resulted in Chao 1 estimating the highest number of species. The incidence-based estimators (Chao 2 and the Jackknives) consistently estimated total richness

TABLE 3. Dissimilarity matrix of Costa Rican altitudinal sites.

	Juan Vinas (1500 m)	Tuis	Turrialba	Guapiles	La Selva
Tuis (732 m)	0.389				
Turrialba (634 m)	0.771	0.758			
Guapiles (259 m)	0.897	0.829	0.960		
La Selva (40 m)	0.718	0.730	0.897	0.769	
Sixaola River (0 m)	0.794	0.781	0.909	0.667	0.571

TABLE 2. Estimated total species richness of *Hemiceras* species for 4 nonparametric estimators.

Species richness estimator	Pakitza Peru	Tambopata Peru	Onkone Gare Ecuador
Observed	36	24	22
Chao 1	43	29	40
Chao 2	39	25	24
1 Jackknife	41	24	24
2 Jackknife	39	25	23

closer to the observed values than did Chao 1, on abundance-based estimates (Table 2).

**Hemiceras faunal comparisons between three tropical regions.** Costa Rica: The high altitude sites of Juan Vinas and Tuis (1500 m and 732 m) were clustered at a dissimilarity value of 0.389, and the low altitude sites (0 m and 40 m) of Sixaola River and La Selva were clustered at a dissimilarity value of 0.571. Guapiles (259 m) was clustered with the low sites at a dissimilarity value of 0.667. The high altitude and low altitude sites were clustered at a dissimilarity value of 0.718. Turrialba (634 m) showed the greatest faunal dissimilarity between all other sites at 0.758 (Table 3; Fig. 4).

Brazil: The two Amazonian sites of São Paulo de Olivença and Porto Velho were clustered at a dissimilarity value of 0.883. Within the Atlantic Coast sites Hansa Humboldt and Santa Catherines were least dissimilar (0.600), Campo Bello was most similar to Hansa Humboldt + Santa Catherines (0.724), and Baixo Guandu was most dissimilar to the previous Atlantic Coast Forest sites (0.833). Dissimilarity between the Amazonia and Atlantic Coast Forests was 0.951 (Table 4; Fig. 5).

Western Amazonia: Pakitza and Tambopata in southeastern Peru were clustered at a dissimilarity value of 0.766. Neblina, Venezuela and Onkone Gare, Ecuador were clustered at a dissimilarity value of 0.793. These four sites were clustered at a dissimilarity value of 0.806. The fauna of São Paulo de Olivença had a dissimilarity value of 0.815 compared to the previous four sites and Porto Velho's fauna was the most dissimilar (0.833) (Table 5; Fig. 6).

TABLE 4. Dissimilarity matrix of comparison of Brazilian Amazonia and Atlantic Coast Forest.

	São Paulo de Olivença	Porto Velho	Baixo Guandu	Campo Bello	St. Catherines
Porto Velho	0.883				
Baixo Guandu	0.982	0.951			
Campo Bello	0.927	0.930	0.833		
St. Catherines	0.945	1.000	0.867	0.724	
Hansa Humboldt	0.958	1.000	0.870	0.792	0.600

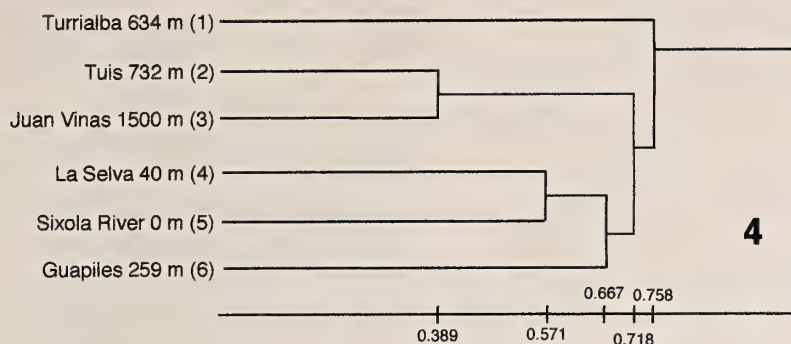


FIG. 4. Dendrogram for cluster analysis of dissimilarity matrix (Table 3) of Costa Rican sites. Numbers refer to localities on Fig. 2. Altitudes are indicated for each site. The scale indicates dissimilarity value.

## DISCUSSION

**Lepidoptera complementarity in SW Amazonia.** The lower complementarity found in most Macrolepidoptera, compared to the Microlepidoptera, may be due to sampling bias; because the collecting was done by UV light, larger moths may be coming from a larger collecting universe than the smaller moths, because the larger species are better able to disperse than the smaller ones. The relatively high complementarity of the Noctuidae is curious given that they are generally strong fliers, medium to large moths, and many species are known for their migration and wide ranging dispersal abilities. The answer may lie in their diversity; because these moths are the most speciose lepidopteran family, the sampling time possible in this preliminary study may be inadequate to accurately assess the ranges of many noctuid species, resulting in a higher complementarity value.

***Hemiceras* species richness in western Amazonia.** To accurately estimate the total number of species of a target taxon (such as *Hemiceras*) at a particular site the species accumulation curve (or the curve of a

suitable richness estimator) should reach an asymptote or remain constant over time with additional sampling. Of the three sites, the species accumulation curve reached an asymptote, only at Pakitza (Fig. 1), suggesting that the species estimate there should be the most accurate. Although Tambopata is known for the high species richness of various insect groups (Fisher 1985, Paulson 1985, Pearson 1985, Wilkerson & Fairchild 1985, Robbins et al. 1996). The *Hemiceras* fauna there is poor, considering that there are 245 species in the neotropics. Although samples taken at Tambopata and Onkone Gare were insufficient to accurately estimate richness, as shown by the non-asymptotic species accumulation curves (Fig. 1), it appears from all the nonparametric estimates, and the steeper accumulation curve, that Pakitza is even richer in *Hemiceras* than is Tambopata. That contrasts with a study of the faunal relationships between the Cicadoidea (Homoptera) (Pogue 1996) and Odonata (Louton et al. 1996) at Pakitza and Tambopata, in which the species richness was greater at Tambopata. Thus, either the preliminary estimate for *Hemiceras* at Tambopata is inaccurate, or this study demonstrates

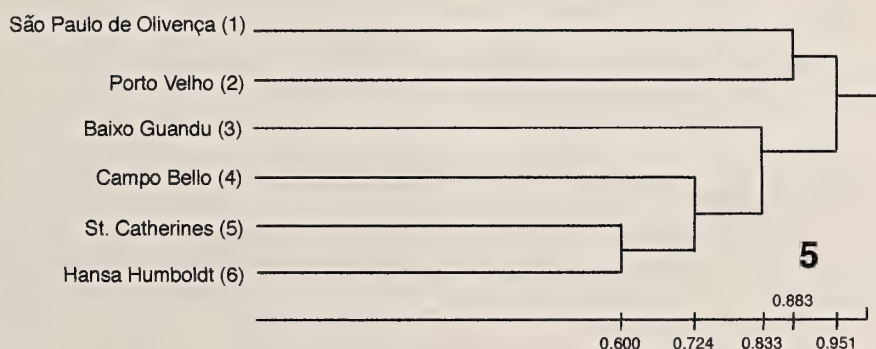


FIG. 5. Dendrogram for cluster analysis of dissimilarity matrix (Table 4) of Brazilian Amazonian and Atlantic Coast Forest sites. Numbers refer to localities on Fig. 3. The scale indicates dissimilarity value.



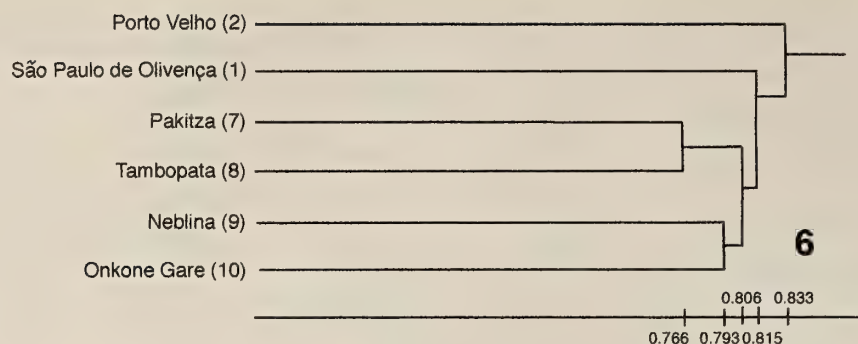


FIG. 6. Dendrogram for cluster analysis of dissimilarity matrix (Table 5) of western Amazonian sites. Numbers refer to localities on Fig. 3. The scale indicates dissimilarity value.

that different taxa, with divergent biologies, have different centers of diversity.

At the Onkone Gare site in Ecuador it is not clear whether the species accumulation curve is approaching an asymptote (Fig. 1) and there are more rare species (12 singletons) than at the other sites, so the prediction of 40 species by Chao 1 (Table 3) may be accurate. Based on the species richness data of *Hemiceras*, the following are recommended for follow-up studies: 1) collecting effort must be adequate for the species accumulation curve, or the estimate curve, to reach an asymptote, 2) if there is a preponderance of rare species, (singletons) Chao 1 should give the highest, and perhaps best estimate, and 3) if the number of rare species is low, Chao 2 or the second-order jackknife may give a better estimate. It is also important to choose your target taxon carefully.

To assess taxon richness, target taxa can be any category, an order, family, subfamily, tribe, or genus. The taxon should be chosen with care. For example, one that is too speciose requires too much time to process and extrapolate the needed data, one with too few species could result in insufficient data. I have found in the Neotropics that a target taxon of 200–400 species seems to be large enough so that the species accumulation curve reached an asymptote after 20–30 samples (trap nights, in this case). The data for the target

taxon can come from collecting, or from using museum collections to obtain faunistic data from specific sites. An advantage of using museum collections are the data available from sites that are no longer pristine, such as those in Amazonia that were collected more than 50 to 100 years ago. Today, with the destruction of the rain forest, these sights will no longer have the same biota. The target taxon has to be common throughout the study area so it can be easily sampled and there should not be a dominance of rare species.

***Hemiceras* faunal comparisons between three tropical regions.** The six sites in Costa Rica show a broad altitudinal range from 0–1500 meters. Altitude seems to influence species composition among sites in Costa Rica more than distance between sites. Juan Vinas (1500 m) and Tuis (732 m) are the highest sites and are clustered at a dissimilarity value of 0.389, the lowest of any pair. If distance was the significant limiting factor of faunal composition, one would expect that Tuis and Turrialba would be clustered. The same is true for the lower altitudinal sites, with La Selva (40 m) and Sixaola River (0 m) having the lower dissimilarity value (0.571), even though La Selva is closer to Guapiles than the Sixaola River site (Table 3) (Fig. 4).

Analysis of the six sites within Brazil were used to show if there was a faunal difference between Amazonia and the Atlantic Coast forest. The Atlantic Coast sites were clustered (Baixo Guandu to Hansa Humboldt) and were quite distinct from the Amazonian fauna (São Paulo de Olivença and Porto Velho) which were also clustered. Within the Atlantic Coast Forest distance seems to be influencing the faunal relationships. Hansa Humboldt and Santa Catherines were most faunistically similar and closest in distance. Campo Bello shows similarity with Hansa Humboldt + Santa Catherines and is closer than Baixo Guandu, which is the most dissimilar and furthest from these

TABLE 5. Dissimilarity matrix of Amazonian sites.

	Neblina	Onkone Gare	São Paulo de Olivença	Porto Velho	Pakitza
Onkone Gare	0.793				
S. P. De Olivença	0.918	0.873			
Porto Velho	0.947	0.886	0.883		
Pakitza	0.860	0.863	0.831	0.833	
Tambopata	0.806	0.821	0.815	0.915	0.766

two sites. Cluster analysis indicates that there is a faunal difference between Amazonia and the Atlantic Coast Forest (Table 4) (Fig. 5).

Amazonia is often treated as one large biogeographical area, but just how different are sites within Amazonia? Among the six Amazonian localities dissimilarities (Table 5) seemed strongly affected by distance and habitat. Pakitza and Tambopata, both in southeastern Peru clustered, as did Onkone Gare, Ecuador and Neblina, Venezuela which are similar in habitat despite being approximately 1160 km distant from each other. Taken together these western Amazonia sites appear to form a region (Fig. 3), perhaps because they lie along the eastern edge of the Andes. Porto Velho was less faunistically similar to São Paulo de Olivença than to Pakitza.

These studies from Costa Rica to Bolivia demonstrate that site-specific data analysis is a prerequisite to a thorough understanding of regional biodiversity patterns. The methods presented above were useful in assessing biodiversity on a site by site basis, and once similar data from other studies and other organisms are pooled, it may be possible to predict complementarity between and among sites and to predict species numbers at other sites. Complementarity, or distinctness of species assemblages among sites can be used with cluster analysis to predict complementarity between a wide variety of parameters such as biogeographic, habitat differences, or host plant specificity. Using species richness estimates, complementarity values, and species lists generated from biodiversity inventories can be useful for biologists and conservationists to make more informed decisions about land use and conservation.

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LETHAL AND NON-LETHAL PARASITOIDS OF *PLATYPREPIA VIRGINALIS* (ARCTIIDAE)

**Additional key words:** Tachinidae, tritrophic interactions, development rate, parasitism.

By definition, a parasitoid is supposed to kill its host (Borror et al. 1989, Ricklefs 1990, Godfray 1994). Previously we reported that *Platyprepia virginalis* Bvd. (Lepidoptera: Arctiidae) caterpillars infected with parasitoids of *Thelaira americana* Brooks (Diptera: Tachinidae) (formerly called *T. bryanti*) often survived the emergence of their flies (English-Loeb et al. 1990, 1993, Karban & English-Loeb 1997). At our study site at the Bodega Marine Reserve, Sonoma County, California (38°19.06'N, 123°4.20'W), caterpillars survived approximately 50% of the time although rates of survival depended upon the host plants and behavior of the caterpillars (English-Loeb et al. 1993, Karban and English-Loeb 1997, Karban 1998). Most early instar *P. virginalis* caterpillars use *Lupinus arboreus* at this study site although *Conium maculatum* is preferred by later instar caterpillars that are parasitized (Karbon & English-Loeb 1997). Caterpillars that survive their parasitoids take longer to develop and pupate at slightly smaller weights than unparasitized caterpillars, although they are reproductively viable (English-Loeb et al. 1990, Karban & English-Loeb 1997). We most commonly observe non-lethal parasitism when we rear caterpillars in the field in large sleeve cages; lab rearings are much more likely to be fatal.

Because non-lethal parasitism is an unusual phenomenon (other examples have been reported for tachinids and caterpillars, e.g., Richards & Waloff 1948, DeVries 1984), we conducted a comparative study to determine what features of this system allowed both the caterpillar and its tachinid parasitoid to survive. We found populations of *P. virginalis* in other locations where caterpillars used different host plants to determine if *T. americana* was ever non-lethal under those circumstances. We also reared 316 individuals of *P. virginalis* outdoors in sleeve cages to determine if other, less common, parasitoid species were ever non-lethal to our host population at the Bodega Marine Reserve.

During 1994 we found populations of *P. virginalis* in riparian habitats of the Trinity Alps (along Rush Creek in Trinity County (40°46.80'N, 122°51.14'W) and along French Creek (40°41.75'N, 122°38.27'W) and Water Gulch (40°40.08'N, 122°42.20'W) in Shasta County, California). We returned to these sites during April 1995, 1996, and 1997 and caged individuals (50 caterpillars in 1995, 75 in 1996, and 44 in 1997) of this inland race on several host plants that were being used naturally by caterpillars at those locations. Our field rearing techniques are described in detail elsewhere (Karbon & English-Loeb 1997).

Of 22 caterpillars that produced adult *T. americana* flies from these inland samples, 10 survived to become adults. This 45% rate of survival is indistinguishable from the 37% survival rate of caterpillars parasitized by *T. americana* during the same three seasons at Bodega (Fisher's exact test,  $n = 60$ ,  $p = 0.59$ ). Survival of both caterpillars and flies from this inland (Trinity Alps) population occurred when caterpillars were reared on *C. maculatum* (2 individuals), *Lupinus albicaulis* (1 individual), and especially *Lupinus albus* (7 individuals). Caterpillars were also reared on *Rubus ursinus*, a commonly used host plant along Rush Creek; of 3 parasitized individuals reared on this host plant, none survived. Caterpillars were found on other host plants including species of *Plantago*, *Phacelia*, *Nemophila*, *Plagiobothrys*, and *Rumex*, although these were not tested as host plants because single individual plants were not large enough to support the complete development of a caterpillar. These observations indicated that the populations of *P. virginalis* and *T. americana* at the Bodega Marine Reserve were not unique in exhibiting non-lethal parasitism. In addition, species of lupine other than *arboreus* could serve as the sole host plants of late instar caterpillars that survived emergence of parasitoids.

Late instar caterpillars (already containing parasitoid larvae) were reared in field cages at the Bodega site in 1987, 1989, 1990, 1991, 1993, 1994, 1995, 1996, and 1997, and at the Trinity Alps sites in 1995, 1996, and 1997. Parasitoids that they contained pupated in these field cages and were collected. Rates of parasitism at Bodega have ranged from 6% in 1996 to 71% in 1990. Most of the para-

sitoids were *T. americana*, although occasionally other species were recovered. We have 5 rearings of *Carcelia reclinata* (A&W), a second tachinid, from *P. virginalis* in the Trinity Alps. This parasitoid was common at our populations in the Trinity Alps in 1994, although we did not rear caterpillars in outdoor cages that season. *C. reclinata* has also been reared from our Bodega population at least 1 time. We reared *Leschenaultia adusta* (Wulp), a very large tachinid, from individuals in our Bodega population on 5 different occasions. We also reared eight individuals of a large ichneumonid wasp, *Ichneumon* sp. from caterpillars at Bodega and from Shasta and Trinity counties. In no case ( $n = 18$ ), did caterpillars recover to pupate successfully after emergence of *C. reclinata*, *L. adusta* or *Ichneumon* sp. During this same period of time (1995–97), 45% of caterpillars with *T. americana* survived to become viable adult moths ( $n = 22$ ). Given the same rate of survival after emergence of *T. americana*, we would have expected 8 caterpillars to have recovered after emergence of the other parasitoids. The likelihood that recovery rates are as high following emergence of these other parasitoids (considered together) as it is following *T. americana* is 0.001 (Fisher's exact test). These results suggest that there is something unique about the interaction between *P. virginalis* and *T. americana* that allows for non-lethal parasitism.

Of these three less common parasitoids, *C. reclinata* seems the most likely candidate to be non-lethal. Because of the low sample size ( $n = 5$ ) of observations of this parasitoid, the likelihood that recovery rates following emergence of *C. reclinata* differ from those of *T. americana* are only 0.12 (Fisher's exact test). More observations of *C. reclinata* parasitizing *P. virginalis* are necessary to determine whether *C. reclinata* can be non-lethal.

What factors could allow *T. americana* but not the other parasitoids to be non-lethal to *P. virginalis*? The ichneumonid is much larger than *T. americana* and remains in the host for longer, often (3 of 8 cases) emerging from the pupa. Lepidopteran larvae sometimes live for days or weeks after emergence of hymenopteran parasitoids although they invariably perish before successfully reproducing (Clausen 1962, Strand et al. 1988). (Hymenopteran parasitoids are much better studied than dipteran parasitoids [Feener and Brown 1997]). Recovering after emergence of *L. adusta*, another tachinid, seems about as unlikely as recovering after the ichneumonid. Like the ichneumonid, *L. adusta* is very much larger than *T. americana* and emerges later, often when the host is beginning to spin its cocoon (3 of 4 cases). *C. reclinata* is a smaller tachinid and can complete its development relatively rapidly. However, in 3 of the 5 cases in which we observed *C. reclinata*, this parasitoid emerged from a caterpillar that was spinning its cocoon. We have noted that the chances that *P. virginalis* will survive the emergence of *T. americana* decrease the later in the development of the caterpillar that parasitoid emergence occurs. One difference between *T. americana* and the other parasitoids that are always lethal is that *T. americana* often completes development during one of the middle stadia of the host larva.

It may be informative to consider the differences from the perspective of the parasitoid's life history traits. Belshaw (1994:149) describes two developmental strategies for tachinids. Some species, perhaps including the ichneumonid and *L. adusta*, delay their own development and only kill their host close to pupation. Selection on these species presumably favors individuals that maximize their size at pupation by consuming most or all of the host. These species will always be lethal. Belshaw describes other tachinids that develop rapidly, often restricting their attack to late instars. *C. reclinata* may fall into this category. Selection on this species presumably favors speed of development or early emergence at the expense of not exploiting all of the host. *T. americana* does not fit this category perfectly because it develops quickly although it attacks early instars. This suggested that *T. americana* that develop rapidly may be more fit than those that take longer. A reanalysis of pupal weights of *T. americana* that developed in *P. virginalis* at Bodega Bay (methods

and data in Karban & English-Loeb 1997) revealed that those that completed development earlier in the season were markedly heavier than those completing development later ( $F_{1,76} = 25.037$ ,  $p < 0.001$ ). This result is consistent with the hypothesis that selection for rapid development at the expense of incomplete host exploitation may sometimes produce non-lethal parasitism. It would be informative to examine whether other tachinids that develop rapidly are also non-lethal.

In conclusion, there does not seem to be anything special about the populations of *P. virginalis*, *T. americana* or the host plants used at Bodega Bay. Non-lethal parasitism was observed for other populations of these insects. However, *T. americana* does appear to be unique among the four parasitoids that attack *P. virginalis* in allowing the host to recover and eventually reproduce. Hopefully these comparisons can be used in the future to elucidate the nature of the interactions that determine lethal and non-lethal parasitism.

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A NEW SYNONYMY IN *DICHRORAMPHA* THAT REVEALS AN OVERLOOKED  
IMMIGRANT RECORD FOR NORTH AMERICA (TORTRICIDAE)

**Additional key words:** *D. vancouverana*, *D. gueneana*, Grapholitini, Olethreutinae, holarctic.

The holarctic genus *Dichrorampha* currently includes nine representatives in North America (Miller 1983, Powell 1983) and several dozen in Eurasia (Obraztsov 1958, Razowski 1996). In revising Palearctic *Dichrorampha*, Obraztsov (1953) proposed the new name *D. gueneana* for a long-known species to which no available name clearly applied. Male *D. gueneana* have a distally upturned valva, a small sharp-pointed process on the ventroposterior edge of the cucullus, and a long, distally curved aedeagus, these characters together forming a diagnostic suite (Figs. 35, 15, respectively, in Obraztsov 1953, 1958; Fig. 4 in Roberts 1991). The sharp-pointed process on the cucullus is sometimes partially obscured in genital slide preparations.

Unknown to Obraztsov, McDunnough (1935) had earlier described the same moth as *D. vancouverana* based on one male captured on Vancouver Island, BC. The *D. vancouverana* holotype male and its genitalia (Fig. 5 in McDunnough 1935) match illustrations and specimens of both Palearctic and Nearctic *D. gueneana* in all respects.

The new synonymy is formalized in the following nomenclatural review.

*Dichrorampha vancouverana* McDunnough

*Dichrorampha vancouverana* McDunnough (1935).

*D. gueneana* Obraztsov (1953). **New Synonymy.**

This new synonymy and specimen examinations resulting from it have four implications beyond taxonomy. (1) *D. vancouverana* is a previously unsuspected immigrant in North America. (2) The year of McDunnough's description of *D. vancouverana*, 1935, is more than five decades earlier than the first published record of *D. vancouverana* in North America (Roberts 1991); Roberts found adults at two Maine sites in 1988 and 1991. (3) The moth occurs in western as well as eastern North America; besides the type specimen from Vancouver, *D. vancouverana* is now recorded from four counties in Washington State, as shown by the specimens enumerated below. These specimens suggest that the species was established in Washington in the 1940s. The moth was not seen there again for half a century; it reappeared during the 1990s in surveys for exotic pests in western Washington (LaGasa 1998, LaGasa et al. 1998). Powell (1988) reported a similar collection hiatus for *Clepsis consimilana* (Hübner), another Pacific Northwest tortricid immigrant. (4) The synonymy brings to 12 the number of North American immigrant tortricids first detected in coastal British Columbia (W. E. Miller unpubl.), a number that spotlights the area as a premier immigrant entry portal.

Larval foodplants of *D. vancouverana* in North America have not been reported, but in Britain and Europe, the larva feeds in rootstocks of milfoil (*Achillea millefolium* L.) and ox-eye daisy (*Chrysanthemum leucanthemum* L.) (both Asteraceae) (Bradley et al. 1979, Kuznetsov 1987). The latter plant has become naturalized in North America (Fernald 1950), and the former also according to some authors (Fernald 1950), but others argue that American *Achillea millefolium* is actually the very similar native *A. lanulosa* Nutt. (Woodward & Rickett 1979).

*D. vancouverana* is widely distributed in the Palearctic (Kuznetsov 1987, Razowski 1996). In the Nearctic, its presently known distribution by states and provinces is British Columbia (McDunnough 1935), Maine (Roberts 1991), New Hampshire (W. Kiel in Winter 1993), New York (R. L. Brown pers. comm.), and Washington State (LaGasa 1998, specimens listed below). As suggested by Roberts (1991), further searching of North American collections might uncover additional specimens and locality records because adults superficially resemble and could be mixed with more common congeners such as *D. sedatana* (Busck). Indeed, R. L. Brown (pers. comm.) recently found *D. vancouverana* specimens captured

in 1975 at Ithaca, New York, thus pushing back the earliest eastern North American record by more than a decade.

Depository abbreviations used in the specimen enumerations below are as follows: CNC, Canadian National Collection of Arthropods, Ottawa, ON; USNM, National Museum of Natural History, Washington, DC; WDA, Washington State Dept. of Agriculture, Olympia. I thank P. T. Dang, Ottawa, ON, J. W. Brown, Washington, DC, and E. LaGasa for the opportunity to examine specimens in their care. I also thank J. A. Powell, D. P. Prowell, and an unnamed reader for useful manuscript reviews, and R. L. Brown and M. A. Roberts for helpful information.

**Specimens examined.** *D. vancouverana* holotype male (CNC); 1 male, "Achil. [probably referring to the *Achillea* foodplant] 4-16-[18]98, Hamfelt Collection" [of known European origin], male genit. slide #2, 2-13-34, C[ar]. H[einrich]., USNM slide 72540; 1 male, "Collection O. Hofmann" [of known European origin], genit. slide # 1, 9-14-22, C[ar]. H[einrich]., USNM slide 72543; 1 male, Sumas, Whatcom Co., WN, 7-12-44, W. H. Baker, Truck Crop No. 5276, genit. slide 12-27-44, C[ar]. H[einrich]., USNM slide 71298; 2 males, Drayton Harbor, Whatcom Co., WN, 7.16.44, W. H. Baker, Truck Crop No. 5278 (diagnostic parts of genitalia revealed by descaling) (all USNM); 1 male, 3.2 km NW Tenino, Thurston Co., WN, 7-9-96, E. LaGasa, genit. slide M 18; 2 females, Port of Seattle, King Co., WN, 7-17 to 28-98, M. Allen (genitalia not examined); 1 male, Shelton, Mason Co., WN, 7-15-98, M. Allen (genitalia not examined) (all WDA).

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"ARGYRESTHIA VISALIELLA CHAMBERS 1875" (ARGYRESTHIIDAE), A NOMEN NUDUM

**Additional key words:** Lepidoptera, North America, taxonomy.

While checking the type localities of species names attributed to Vactor T. Chambers for an annotated checklist of Kentucky Lepidoptera, I encountered a name that stands in synonymy of *Argyresthia apicimaculella* Chambers 1874 (Argyresthiidae; type locality: "Kentucky"). The name is "*visaliella* Chambers 1875," as the two names are listed as entry #2438 in Hodges et al. (1983).

This same synonymy appears as #6456 in Dyar ("1903" [1904]) along with a page reference to Chambers' presumed original description; however the publication date is quoted erroneously by Dyar as "1874." In that 1875 paper we find not an original description of *visaliella* but a reference to it in the discussion of "*Argyresthia goedartella* Auct." in which Chambers states, after describing a specimen presumed to be that species, "It is a more handsome species than *A. andereggiella*, next after which as to beauty I would place *A. visaliella* Cham."

In searching for the original description of "*A. visaliella*" I found only one "*visaliella*"—that of Chambers 1873, p. 113, described in *Cyane* Chambers, but listed in Hodges et al. (1983) #307 as *Choropleca vesaliella* [sic] (Cham. 1873). The type locality of this name is Visalia, Kentucky, which is in Kenton County not far south of Chambers' home town of Covington. Chambers wrote "Several specimens captured in June resting on forest trees at Visalia, Kentucky." This constitutes a rare specific type locality published by Chambers.

Thus it appears that "*A. visaliella* Chambers" is a *nomen nudum*. Also the name *Choropleca visaliella* (Cham. 1873) is misspelled in Hodges et al. (1983) and was also misspelled in Forbes (1923).

I thank Ronald W. Hodges and Paul A. Opler for reviewing this manuscript.

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ERRATA

STUDIES IN THE GENUS *HYLEPHILA* BILLBERG, I. INTRODUCTION AND THE *IGNORANS* AND *VENUSTA* SPECIES GROUPS (HESPERIIDAE: HESPERIINAE)

In the above paper by C. D. MacNeill and J. Herrera G. (Journal of the Lepidopterists' Society 52(3):277–317) there were two typographical errors in the text:

pp. 283–287. The legends for Figures 4, 5, 6, 7, and 8 should read

"... (descaled to show caudal array of tuberculate bristle-sockets at 70× with inset enlarged below), ..."

pp. 316, lines 7 and 8. The reference should read:

\_\_\_\_\_. 1940. Hesperioidea XI. Especies nuevos para nuestra fauna y anotaciones sobre otros. Rev. Soc. Entomol. Argent. 10:279–297, figs. 8, 9.

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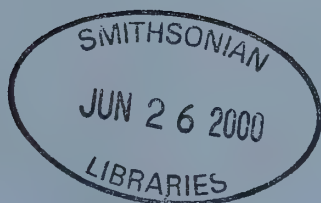
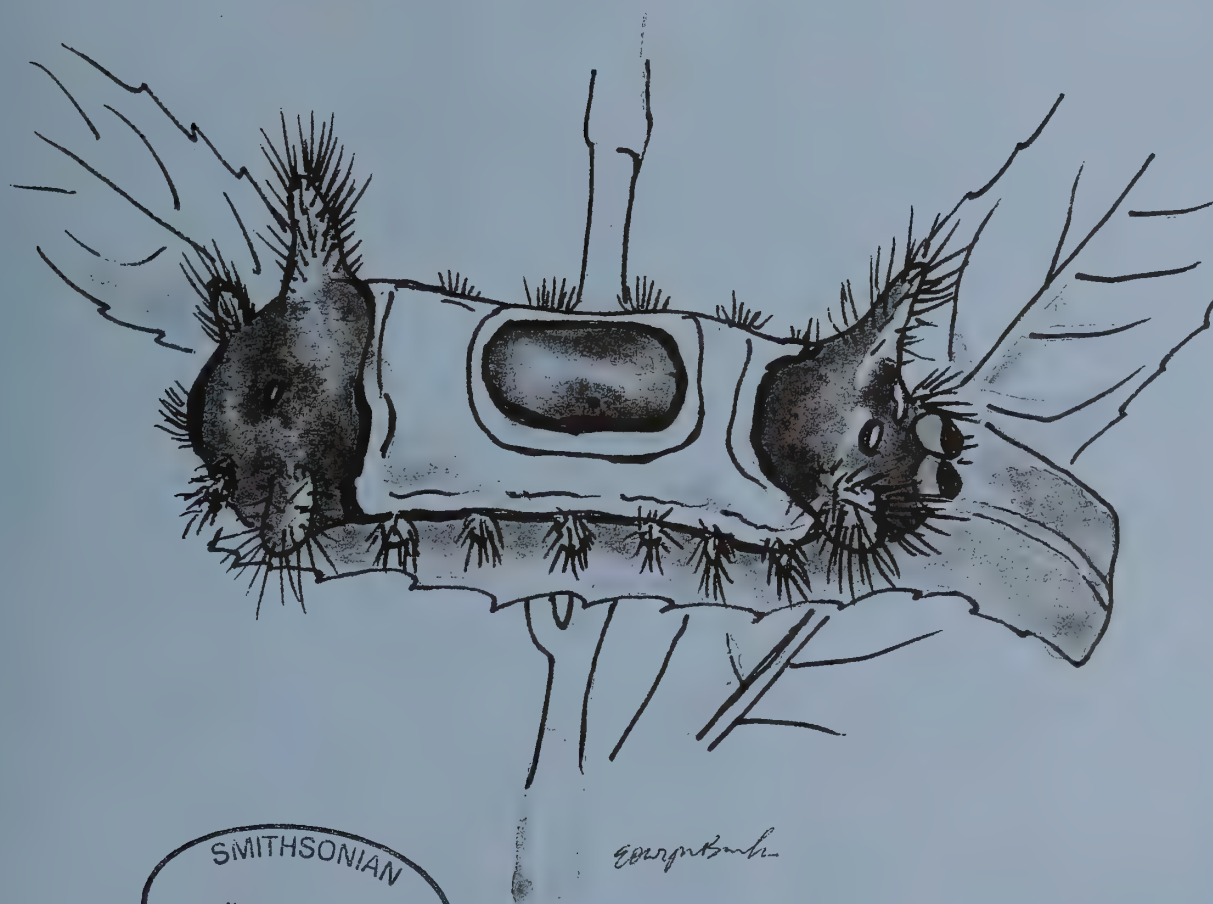
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# JOURNAL OF THE LEPIDOPTERISTS' SOCIETY

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## DREPHALYS: DIVISION OF THIS SHOWY NEOTROPICAL GENUS, PLUS A NEW SPECIES AND THE IMMATURES AND FOOD PLANTS OF TWO SPECIES FROM COSTA RICAN DRY FOREST (HESPERIIDAE: PYRGINAE)

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**ABSTRACT.** Mainly on the basis of many male and female genitalic characters, *Drephalys* splits cleanly into two subgenera: *Drephalys* (*Drephalys*) Watson 1893 (= *Paradros* Watson 1893), with at least 16 species, and ***Drephalys* (*Paradrephalys*) Burns, new subgenus** (type species *Hesperia dumeril* Latreille 1824), with at least 7 species. Although these showy, diurnal, neotropical pyrgine hesperiids generally are rare in collections, two species have been reared repeatedly in the tropical dry forests of the Area de Conservacion Guanacaste (ACG) in northwestern Costa Rica: ***Drephalys* (*Drephalys*) *kidonoi* Burns, new species**, and *D. (D.) alcmon* (Cramer). In the ACG, larvae of *D. kidonoi* (N = 236) eat *Roupala montana* Aublet (Proteaceae), and larvae of *D. alcmon* (N = 70) eat *Hirtella racemosa* Lamarck (Chrysobalanaceae). In Panama, as well, *D. alcmon* eats *Hirtella racemosa*; but in Pará, Brazil, it eats the *Hirtella* relatives *Couepia* and *Parinari* (Chrysobalanaceae), whereas *D. (D.) eous* (Hewitson) eats *Vochysia vismiaeifolia* Spruce (Vochysiaceae). As far as we can tell (admittedly not far), different species of *Drephalys* (*Drephalys*) seem to be specializing on food plants in taxonomically unallied families. Larvae of these three *Drephalys* (*Drephalys*) species share a basically similar color pattern, which is distinctive. With a development time of 45–55 days from newly-eclosed larva to prepupa, *D. kidonoi* is one of the slower-growing of some 190 species of pyrgines reared in the ACG. Adults of *D. kidonoi* apparently breed chiefly during the first half of the dry season, when other dry-forest skippers have emigrated or are sexually dormant. While *D. kidonoi* still is known only from Guanacaste, Costa Rica, *D. alcmon* ranges far more widely—from eastern Peru and central Brazil all the way to Guatemala, at least (it has not previously been reported from Central America). Despite close genitalic similarities that mark *D. kidonoi* as the sister species of *D. helixus* (the type species of *Drephalys*), *D. kidonoi* departs sharply in color pattern from it and all other species of *Drephalys*, apparently to mimic several common species of the silver-spotted skippers *Epargyreus* with which it is sympatric. We illustrate comparatively the larvae, pupae, adults, and genitalia of species of *Drephalys* (*Drephalys*) that are central to this paper.

**Additional key words:** *Drephalys* (*Drephalys*) *alcmon*; *Drephalys* (*Drephalys*) *kidonoi* Burns, new species; *Drephalys* (*Paradrephalys*) Burns, new subgenus; *Hirtella racemosa* (Chrysobalanaceae); *Roupala montana* (Proteaceae).

Once more, taxonomy and ecology join forces for the greater good.

A several-decade inventory of Lepidoptera larvae in the tropical dry forests of the Area de Conservacion Guanacaste (ACG) in northwestern Costa Rica (Janzen & Hallwachs 1998) currently is focusing on the HesperIIDae or skipper butterflies (Burns & Janzen in prep.). Of some 190 species of pyrgine hesperiids now reared, at least two are new. The first, *Cephise nuspesez* Burns, joined a number of “known” species—which were buried in the wrong genus or in synonymy—to swell *Cephise* from a monotypic to a polytypic neotropical genus, tightly characterized by many aspects of

genitalic form (in both sexes), by a unique feature of the labial palpus, and by shared larval food plants (in the Malpighiaceae and Combretaceae) (Burns 1996). The fact that some species of *Cephise* have long hind-wing tails while others do not, may explain why these skippers had never been seen as related, much less congeneric; but presence or absence of tails, though striking, can be taxonomically trivial. The second reared new species, *Drephalys kidonoi*, debuts here.

Because one ought not describe a new species without considering its taxonomic setting, Burns examined the genus *Drephalys* in as much detail as available material would allow. Unfortunately, this neotropical



genus of showy, medium large skippers is remarkably rare in collections. To illustrate, when Evans (1952) treated *Drephalys* (the most recent overall review), he included two taxa that were not represented in the vast hesperiid holdings of The Natural History Museum (BMNH); and he described three new species from single (or, in one case, a pair of) specimens. Evans also described what he called a new subspecies (*D. orian-der oria*, from Honduras) from just 3 specimens (*oria* Evans is actually a separate species, distinct from *oriander* [Hewitson] though related to it). One of the two new species of *Drephalys* that Mielke (1968) described from far southeastern Brazil (Santa Catarina) was based on a single male. One of the two new species that Austin (1995) described from westcentral Brazil (Rondônia) was based on 4 specimens. In reviewing a meager accumulation of *Drephalys* to develop a context for *D. kidonoi*, Burns already has discovered five more new species, represented by scant samples of 8, 6, 3, 1, and 1.

In sharp contrast, we have a huge sample of *D. kidonoi*—the type series amounts to 53 adults from Guanacaste—obtained almost entirely by rearing from 236 larvae found in nature. (Adults are far fewer than larvae because, in the course of rearing, many larvae were lost to parasitoids, fungi, and other diseases; and because some healthy reared adults were released.) Even though the larvae can be located with fair ease, only one adult has been caught in the wild. This, along with the general scarcity of *Drephalys* in collections, suggests adult behavior that tends to keep the skippers and their potential human captors apart. However, *Drephalys* is definitely diurnal, not crepuscular and/or nocturnal like some tropical skippers; and males are known to hilltop, though only for a very limited and specific period in any given day (Mielke 1968, pers. comm., Casagrande & Mielke 1992).

Watson (1893:34) proposed the genus *Drephalys* (with the type species *helixus* Hewitson) but did not define it well. Eleven genera later in the same paper, Watson (1893:39) also proposed the genus *Paradros* (with the type species *phoenice* Hewitson). Godman and Salvin (1894:349) immediately set these genera side by side, observing "There can be no doubt that *Drephalys* should be placed next *Paradros*, and the only question that arises is whether these two genera ought not to be merged into one." While Mabille and Boullet (1919) still kept them separate but adjacent, Evans (1952:23) correctly listed *Paradros* as a synonym of *Drephalys*, remarking that "Typically these 2 genera appear very different, but they are connected by intermediate species and the genitalia conform to a general pattern." Although his statement is partly true,

*Drephalys* as treated by Evans is gravely polyphyletic. Burns (1999) addressed this problem by removing morphologic misfits to the new and unrelated genus *Pseudodrephalys*.

Any lingering questions about the generic limits of *Drephalys* have no bearing on the inclusion of *kidonoi* for the simple reason that *kidonoi* is the sister species of *helixus*. Since *helixus* is the type species of *Drephalys*, the sister species *kidonoi* must also go in *Drephalys*. It will be treated together with *helixus* to document their similarity.

*Drephalys heraclides* Bell (1942:1), which is yet another species described from a single male (this time from "Peru"), was said in the original description to be "extremely like *helixus*." Though Bell further noted that "The form of the male genitalia is similar in the two species, but the details materially differ," he did not elaborate. Still known only from the holotype, *heraclides* is one of those taxa Evans (1952) never saw; and, as a result, he conservatively called it a subspecies of *D. helixus*. This is wrong. Study of the holotype of *heraclides* (borrowed from AMNH) and of Bell's (1942:fig. 1) illustration of its genitalia (because the slide of its genitalia has been lost) shows not only that *D. heraclides* is a distinct species of *Drephalys* but also that it is morphologically farther from *D. helixus* than is *D. kidonoi*.

In connection with five species of *Drephalys* occurring in Rondônia, Brazil, Austin (1995:127) commented that "There appear to be a number of species groups in *Drephalys* with quite different genitalia of both sexes." Even after Burns's (1999) transfer of a pair of incredibly misplaced species—*atinas* (Mabille) and *hypargus* (Mabille)—from *Drephalys* to the distant new genus *Pseudodrephalys*, *Drephalys* is genitally complex. This complexity can be resolved into two readily characterizable groups that are highly distinct. Despite their differences, each is apparently the other's nearest relative; so at this point in the analysis of hesperiid biodiversity, it is better to treat them as subgenera than as separate genera. A similarly cautious approach was taken in recognizing—but not overemphasizing—two useful, valid, well-differentiated divisions of the dusky wing skippers of the genus *Erynnis*: *Erynnis* (*Erynnis*) and *Erynnis* (*Erynnides*) (Burns 1964).

*Drephalys* (*Drephalys*) Watson, 1893:34  
= *Paradros* Watson, 1893:39.

**Type species.** *Eudamus helixus* Hewitson (1877:320).

**Male genitalia.** Uncus with pair of caudally projecting prongs that form **U** (Figs. 1, 3) or **V** in dorsal or ventral view. In lateral view, juxta either at level of vinculum or considerably anterior to it (Figs. 2, 4). If present, any dorsal projection from sacculus (i.e., sclero-



TABLE 1. Species of *Drephalys* (*Drephalys*).

<i>alcmon</i> (Cramer)	<i>olva</i> Evans
<i>eous</i> (Hewitson)	<i>olvina</i> Evans
<i>helixus</i> (Hewitson)	<i>opfex</i> Evans
<i>heraclides</i> Bell	<i>phoenice</i> (Hewitson)
<i>kidonoi</i> Burns	<i>phoenicoides</i> (Mabille & Bouillet)
<i>miersi</i> Mielke	4 undescribed species
<i>mourei</i> Mielke	

tized, anteroventral portion of inner lamina of valva) arises from proximal part of sacculus (Figs. 2, 4); apart from this projection, sacculus slopes sharply downward from anterior to posterior in lateral view (Figs. 2, 4). At least slightly dentate process arising from distal end of valva curves mostly mediad (Figs. 1, 3), but sometimes also dorsad (Figs. 2, 4) or caudad (or even cephalad so as to be recurved). Below this dentate, medially curved process, ventrodistal corner of valva usually rounded and extended slightly (Figs. 2, 4) to moderately caudad, but sometimes prolonged into blunt point. Above the dentate, medially curved process, dorsodistal corner of valva ranges from completely undeveloped or slightly developed (Figs. 1–4) to a small to large process, variable in orientation and degree of dentation (rarely none). Aedeagus with very short to very long subterminal to terminal (Figs. 1–4) titillator on left side. Vesica long, delicate, fingerlike, with 1–14 needlelike cornuti (almost always in cluster) at distal end (Figs. 1, 3). In dorsal or ventral view, anterior end of saccus pointed (Figs. 1, 3), keeled, or narrowly rounded.

**Female genitalia.** Posterior portion of ductus bursae, which is well-sclerotized, extending well anterior of sterigma (Figs. 5–8) and flattened dorsoventrally, at least anterior (Figs. 6, 8). Thereafter, ductus bursae both narrow and long (Figs. 5–8). Altogether, bursa copulatrix takes rather indirect course from posterior to anterior (Figs. 5–8) (except in some individuals of *D. alcmon* [Cramer] and presumably also *D. mourei* Mielke [female unknown]). Lamella antevaginalis and lamella postvaginalis distinct from each other (Figs. 5–8) rather than fused and inseparable. Lamella antevaginalis a more or less simple, narrow band which may (Figs. 5–8) or may not be sclerotized midventrally; it forms conspicuous, paired, more or less caudally pointing, sharp projections immediately lateral to ostium bursae (Figs. 5–8) (except in *D. alcmon* and presumably *D. mourei*). Lamella postvaginalis a ventrally convex plate with midventral **U** or **V** in its posterior margin (Figs. 5–8).

**Costal fold of male.** Well-developed to vestigial or absent.

**Wingshape.** Hindwing elongate (Figs. 9–20), appreciably longer than wide (more so in males [Figs. 9, 10, 13, 14, 17, 18] than in females [Figs. 11, 12, 15, 16, 19, 20]), and clearly lobed at end of vein 1b (Figs. 9–16, 19, 20) [lobes of male in Figs. 17, 18 damaged].

**Included species.** N = 16 (Table 1).

### *Drephalys* (*Paradrephalys*) Burns, new subgenus

**Type species.** *Hesperia dumeril* Latreille (1824:757).

**Male genitalia.** Uncus truncate, with no long caudally projecting prongs in dorsal or ventral view. In lateral view, juxta begins at level of vinculum and extends posteriorly beneath aedeagus. Tall, dorsal projection arises from distal part of sacculus (i.e., sclerotized, anteroventral portion of inner lamina of valva); apart from this projection, sacculus nearly or quite uniform in height from anterior to posterior in lateral view. Process arising from middle part of dorsal margin of valva extends mostly caudad, usually becoming at least slightly dentate distally. Narrow, slightly dentate process arising from distal end of valva extends mostly dorsad to overlap aforementioned process. Valva at its ventrodistal corner so totally undeveloped as to be “chinless” in lateral view. Aedeagus short, relatively stout, and devoid of titillators (although sometimes very finely dentate ventrolaterally or midlaterally, on one or both sides, slightly before its posterior tip). Short, fat vesica everts caudally but especially to right and sports numerous (11–33) needlelike cornuti in several loose assem-

TABLE 2. Species of *Drephalys* (*Paradrephalys*).

<i>croceus</i> Austin	<i>talboti</i> (Le Cerf)
<i>dumeril</i> (Latreille)	<i>tortus</i> Austin
<i>oria</i> Evans	1 undescribed species
<i>oriander</i> (Hewitson)	

blages. In dorsal or ventral view, anterior end of saccus expanded or broadly rounded.

**Female genitalia.** Posteriormost portion of ductus bursae a cylindrical tube, well-sclerotized—except for broad, middorsal, clear strip—and so short that it extends only slightly anterior of sterigma. Sterigma reflects major fusion between lamellae antevaginalis and postvaginalis. At posterior end of ductus bursae, parts of lamella antevaginalis that are closely appressed to its sides meet midventrally to form (in ventral view) a large **U** or **V** (which opens caudally) just ventrad of ostium bursae. Posterior to this, lamella postvaginalis forms another large (and similarly oriented) midventral **U** or **V**. All of the above framed laterally by paired, (essentially) parallel, large, thin, vertical plates extending ventrad from sterigma (so as to be seen on edge in ventral view). Although these long, thin plates closely flank the central equipment, they leave a deep fissure on either side of it. Immediately dorsal and lateral to all of above—about halfway up sides of sterigma—a conspicuous, somewhat fingerlike and caudally pointing, unsclerotized area extends two-thirds distance from anterior to posterior margin of sterigma. Seen ventrally, entire sterigma tends to look long, narrow, and more or less rectangular. Immediately anterior of point where posterior sclerotized tube of ductus bursae becomes membranous, ductus swells to large sac (which may have folded, sclerotized plate in its walls) and then constricts sharply before expanding anterior into corpus bursae. Altogether, bursa copulatrix takes rather direct course from posterior to anterior.

**Costal fold of male.** Well-developed.

**Wingshape.** Hindwing roundish, nearly as wide as long (more so in females than in males), and barely lobed at end of space 1b.

**Included species.** N = 7 (Table 2).

### The *helixus/kidonoi* species pair of *Drephalys* (*Drephalys*)

**Male genitalia.** Dorsal projection arising from proximal part of sacculus uniquely long from anterior to posterior and finely dentate dorsally (Figs. 2, 4). In dorsal or ventral view, saccus tapers anterior to extremely delicate, sharp point (Figs. 1, 3). In lateral view, distal end of valva roughly truncate, with no major development of dorsodistal corner, but with narrow, finely dentate process (which extends mediad, dorsad, and caudad) arising closer to ventrodistal corner of valva than to dorsodistal corner (Figs. 2, 4).

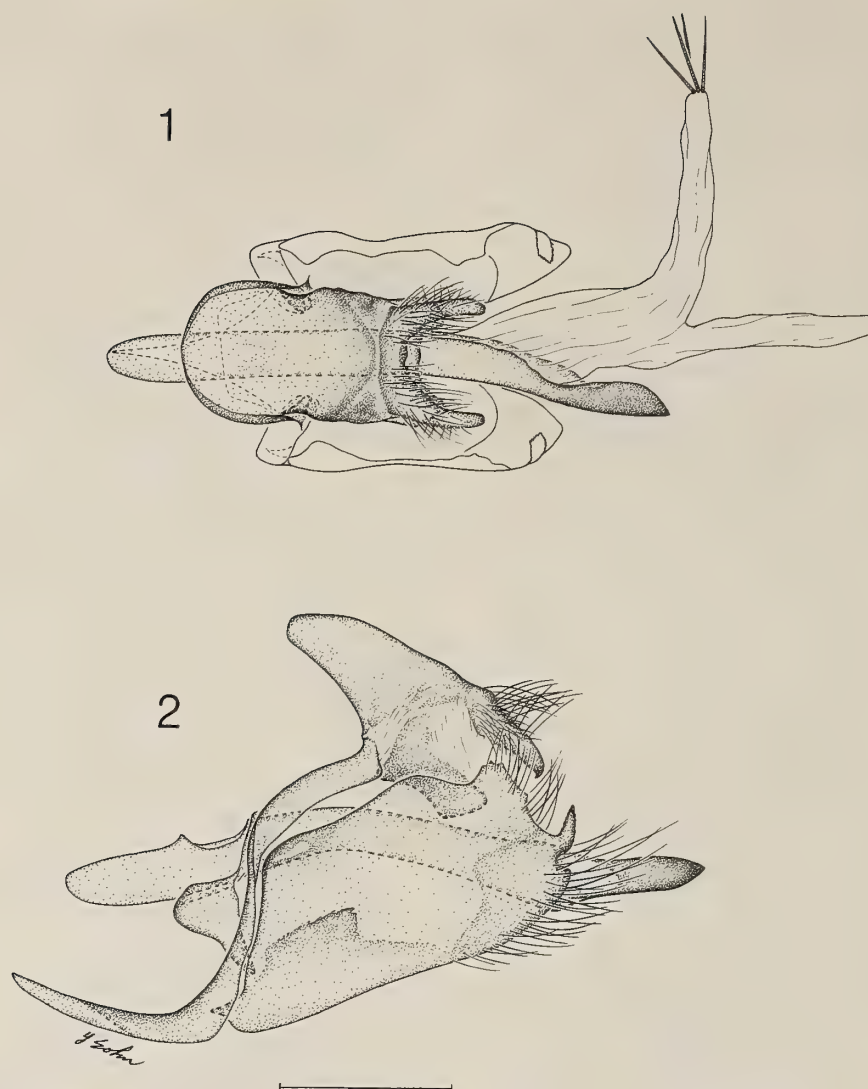
**Female genitalia.** Anterior, where the well-sclerotized posterior portion of the ductus bursae abruptly becomes membranous and sharply decreases in diameter, a large, blind, membranous sac extends at least slightly to the right; and the narrowed, membranous ductus bursae angles dorsad, perpendicular to its sclerotized course, before continuing anterior to the corpus bursae (Figs. 5–8).

**Costal fold of male.** Narrow (*helixus*) or almost vestigial (*kidonoi*).

**Number of antennal nudum segments.** High (Table 3). Although there are too few specimens of other species of *Drephalys* to include the conspicuously variable nudum in the preceding subgeneric characterizations with confidence, there are enough to indicate that the mean number of nudum segments is greater in *helixus* and *kidonoi* than it is in other species of *Drephalys*. Moreover, the mean number of nudum segments is clearly greater in females than it is in males (Table 3). Evans (1952:6) said for *Drephalys* “Nudum typically 16/15, arcuate or hooked”; but his total of 31 segments is a little too low to be typical for this genus.

**Palpus.** Third segment of palpus (which in *Drephalys* and its relatives is not centered on the second segment but, instead, shifted





FIGS. 1, 2. Male genitalia of *Drephalys (Drephalys) kidonoi* (paratype) from the Area de Conservacion Guanacaste, Guanacaste, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 92-SRNP-445) (J. M. Burns genitalic dissection no. X-3422) (USNM); scale = 1.0 mm. **1**, Tegumen, uncus, gnathos, and aedeagus [all stippled] with everted vesica and cornuti (plus cut, everted sperm duct), as well as both valvae, vinculum, juxta, and saccus [all outlined] in dorsal view. Rotating the genitalia until the top of the tegumen/uncus is about flat makes the underlying structures look shorter than they do in the lower figure (but the scale is the same in both figures). **2**, Complete genitalia (minus right valva and everted vesica and cornuti) in left lateral view.

conspicuously laterad—see Burns 1999:figs. 19, 20) unusually short, protruding less far anteriorly of second segment than in other species of *Drephalys*. (Note that in *Drephalys* generally, the third segment of the palpus is shorter in males than it is in conspecific females.)

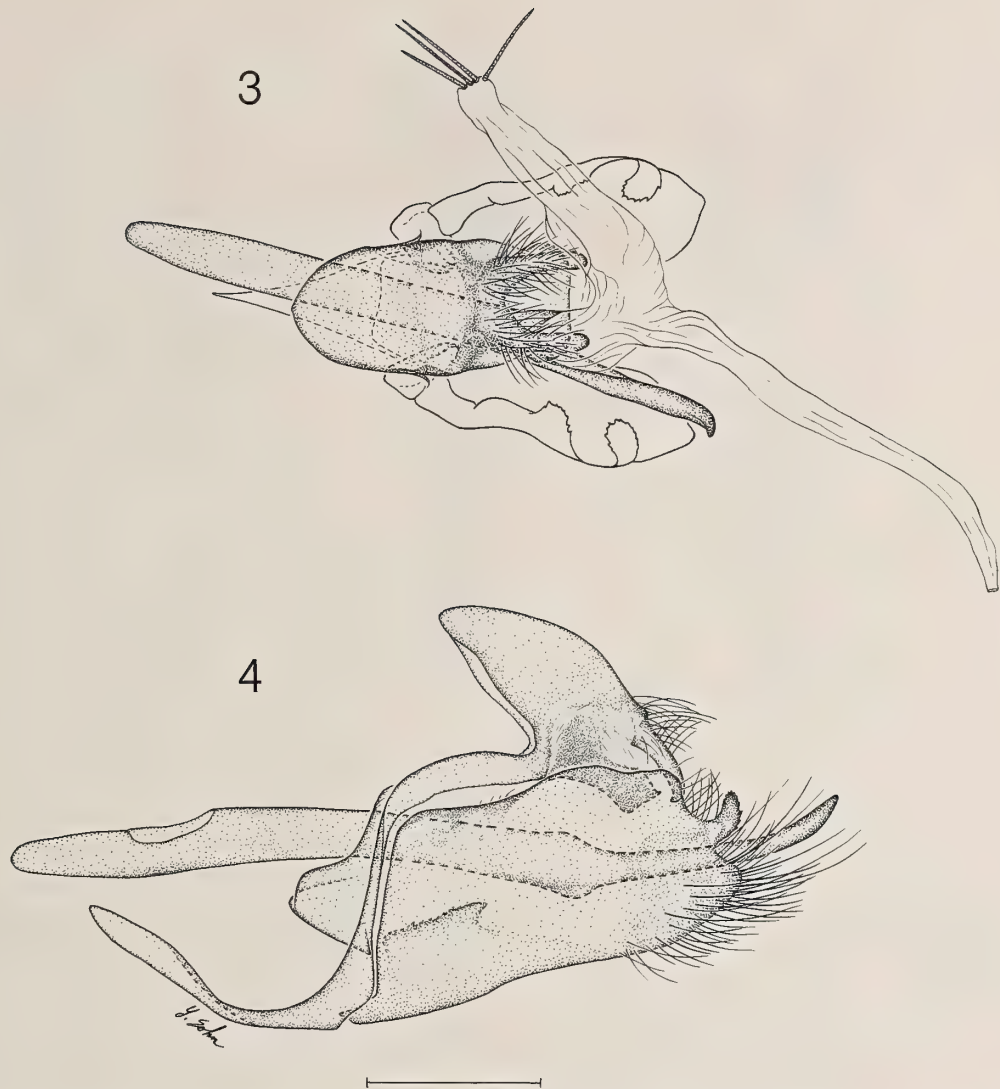
TABLE 3. Number of antennal nudum segments in sister species of *Drephalys (Drephalys)*.

Species	Sex	N	Range	Mean
<i>D. helixus</i>	♂	18	33–37	35.3
"	♀	1	40	40
<i>D. kidonoi</i>	♂	27	30–42	35.0
"	♀	22	34–51	40.8

**Size.** Among the larger species of *Drephalys*. As usual in hesperiids, males average smaller than coexisting females (Table 4). Although *helixus* from Panama looks a little larger than *kidonoi* (Table 4), the difference may not be real: all specimens of *helixus* are wild-caught whereas all measured specimens of *kidonoi* are reared, with the likely result that most are appreciably stunted.

### *Drephalys (Drephalys) kidonoi* Burns, new species

**Male genitalia.** Aedeagus shorter than that of *helixus*, owing mainly to titillator. Titillator (i.e., caudal extension of left side of aedeagus, beginning where vesica emerges) shorter by half, as well as stouter (Figs. 1, 2), than that of *helixus* (Figs. 3, 4) and not turned slightly up at distal end. Saccus also shorter (a condition almost certainly correlated with the reduced aedeagal length). Body of aede-



FIGS. 3, 4. Male genitalia of *Drephalys* (*Drephalys*) *helixus* from Rodman, 8°58'N 79°35'W, Canal Zone, PANAMA, 22 December 1972 (G. B. Small) (J. M. Burns genitalic dissection no. X-4254) (USNM); scale = 1.0 mm. **3**, Tegumen, uncus, gnathos, and aedeagus [all stippled] with everted vesica and cornuti (plus cut, everted sperm duct), as well as both valvae, vinculum, juxta, and saccus [all outlined] in dorsal view. Rotating the genitalia until the top of the tegumen/uncus is about flat makes the underlying structures look shorter than they do in the lower figure (but the scale is the same in both figures). The oblique position of the aedeagus is unnatural. **4**, Complete genitalia (minus right valva and everted vesica and cornuti) in left lateral view.

gus, in lateral view (Fig. 2), bowed more dorsad than in *helixus* (Fig. 4). Process arising from distal end of valva a little less conspicuously dentate (Figs. 1, 2) than in *helixus* (Figs. 3, 4) and straight along its dorsal margin (Figs. 1, 2) rather than slightly convex as in *helixus* (Figs. 3, 4).

TABLE 4. Forewing length (mm) in sister species of *Drephalys* (*Drephalys*).

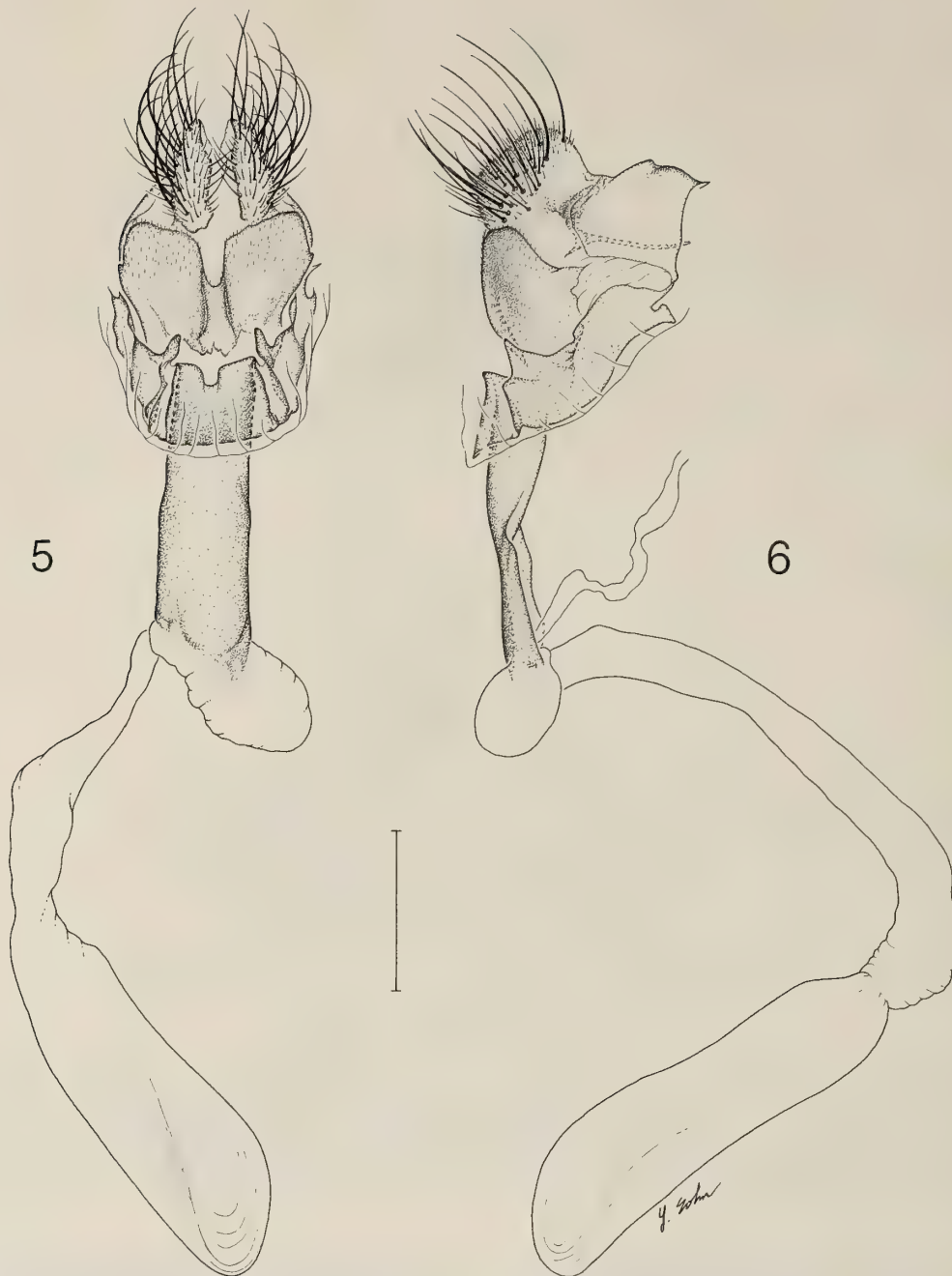
Species	Locality	Sex	N	Range	Mean
<i>D. helixus</i>	Brazil	♂	3	22.7–23.9	23.20
"	Panama	♂	15	20.6–22.2	21.49
"	"	♀	1	23.6	23.6
<i>D. kidonoi</i>	Costa Rica	♂	28	17.0–22.0	20.22
"	"	♀	24	19.0–24.7	22.22

**Female genitalia.** Lamella postvaginalis deeply notched mid-ventrally in its posterior margin and grooved midventrally along its entire length (Fig. 5) rather than shallowly notched and grooveless as in *helixus* (Fig. 7). Immediately farther anterior, at posterior end of ductus bursae, at least a small midventral notch (Fig. 5) not present in *helixus* (Fig. 7). Sclerotized portion of ductus bursae flattened dorsoventrally in its anterior half (Fig. 6) instead of its anterior two-thirds as in *helixus* (Fig. 8). Paired, caudally pointed projections from lamella antevaginalis (immediately lateral to ostium bursae) shorter, less delicate, and originating farther posterior (Figs. 5, 6) than in *helixus* (Figs. 7, 8).

**Costal fold of male.** Present but exceedingly narrow (much narrower than that of *helixus*)—almost vestigial.

**Facies/mimicry.** Unique among species of *Drephalys*: *kidonoi* (Figs. 9–12) departs sharply from a more usual *Drephalys* appearance (as, for example, in *helixus* [Figs. 13–16]) to suggest several

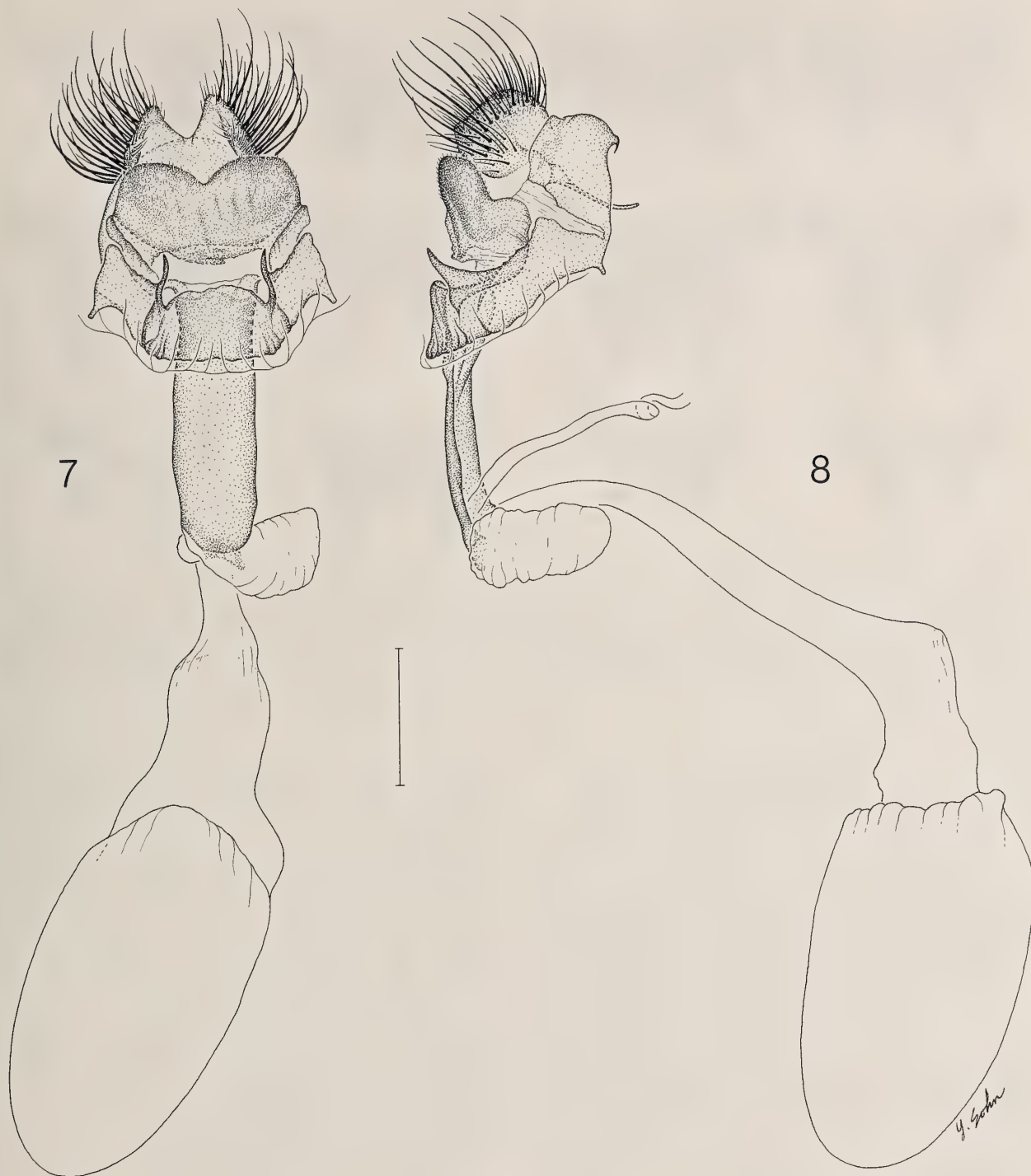




FIGS. 5, 6. Female genitalia of *Drephalys (Drephalys) kidonoi* (paratype) from the Area de Conservacion Guanacaste, Guanacaste, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 92-SRNP-480) (J. M. Burns genitalic dissection no. X-3423) (USNM); scale = 1.0 mm. **5**, Ovipositor lobes, sterigma, and bursa copulatrix in ventral view. **6**, The same, plus part of the ductus seminalis, terminal abdominal tergite, and posterior apophysis, in right lateral view.

common species of the silver-spotted skippers *Epargyreus* with which it is sympatric. On the forewing, this involves (a) eliminating (Figs. 9–12) the spot in space 1b (Figs. 13–20); (b) reducing to tiny points or, more often, completely eliminating (Figs. 9–12) the small subapical spots in spaces 6, 7, and 8 (Figs. 13–20); (c) reducing (Figs. 11, 12) or eliminating (Figs. 9, 10) the outer cell spot (Figs. 13–20); and (d) suppressing (Figs. 10, 12) the yellow coloration along the proximal half of the ventral costal margin (Figs. 14, 16, 18,

20). On the hindwing, this involves (dorsally) more or less suppressing (Figs. 9, 11) what is normally a conspicuous double row of spots (Figs. 13, 15); and (ventrally) shortening and making less regular (Figs. 10, 12) a conspicuous central white stripe (Figs. 14, 16). On both wings, this involves (dorsally) intensifying the color of proximal scales—to an orangy yellow—to heighten the contrast with more distal ones (Figs. 9, 11); and (ventrally) adding lavender overscaling broadly along the outer margins (Figs. 10, 12). The total effect is one



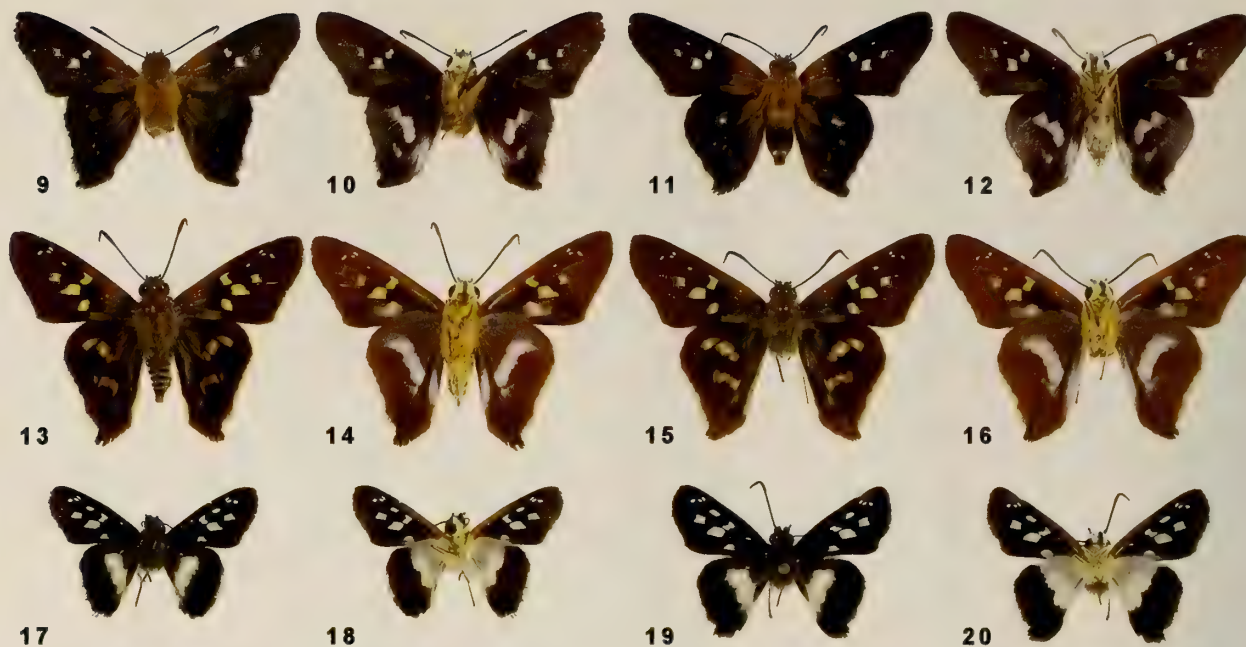
FIGS. 7, 8. Female genitalia of *Drephalys* (*Drephalys*) *helixus* from Rodman Naval Station, Canal Zone, PANAMA, 9 January 1972 (S. S. Nicolay) (J. M. Burns genitalic dissection no. X-4263) (USNM); scale = 1.0 mm. **7**, Ovipositor lobes (by chance, wider apart than in Fig. 5), sterigma, and bursa copulatrix in ventral view. **8**, The same, plus part of the ductus seminalis, terminal abdominal tergite, and posterior apophysis, in right lateral view.

of apparent mimicry. Because the hindwing is a little less elongate in *kidonoi* (Figs. 9–12) than it is in *helixus* (Figs. 13–16), *kidonoi* even approaches the wingshape of *Epargyreus*.

**Larval food plant.** *Roupala montana* Aublet (Proteaceae).

**Types.** *Holotype*: COSTA RICA, PROVINCIA GUANACASTE, Area de Conservacion Guanacaste, Sector Poco Sol, Poco Sol, 270 m, Janzen & Hallwachs rearing voucher 91-SRNP-2736, adult emergence date 20 Feb 1992, ♂, genitalia no. X-4243 J. M. Burns 1997;





FIGS. 9–20. Males and females of *Drepthalys* (*Drepthalys*) from the Area de Conservacion Guanacaste, Guanacaste, COSTA RICA (reared) and from Rodman, Canal Zone, PANAMA (wild-caught) in dorsal (odd-numbered) and ventral (even-numbered) views ( $\times 0.85$ ) (all USNM). **9, 10**, *D. kidonoi* ♂, holotype, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 91-SRNP-2736) (J. M. Burns genitalic dissection no. X-4243). **11, 12**, *D. kidonoi* ♀, paratype, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 92-SRNP-345). **13, 14**, *D. helixus* ♂, PANAMA, 28 November 1974, G. B. Small. **15, 16**, *D. helixus* ♀, PANAMA, 9 January 1972, S. S. Nicolay (J. M. Burns genitalic dissection no. X-4263). **17, 18**, *D. alcmon* ♂, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 96-SRNP-1047) (J. M. Burns genitalic dissection no. X-4245). **19, 20**, *D. alcmon* ♀, COSTA RICA (D. H. Janzen & W. Hallwachs rearing voucher no. 96-SRNP-1090) (J. M. Burns genitalic dissection no. X-4249).

deposited in National Museum of Natural History, Smithsonian Institution (USNM).

*Paratypes*  $N = 52$  (27 ♂, 25 ♀). *Reared Paratypes (with emergence dates)*: COSTA RICA, PROVINCIA GUANACASTE, Area de Conservacion Guanacaste: Sector El Hacha, Casa Oeste, 420 m, 93-SRNP-8708, 21 Jan 94, ♀; 93-SRNP-8712, 17 Mar 94, ♂; 93-SRNP-8738, 22 Jan 94, ♀; 93-SRNP-8740, 17 Jan 94, ♂; 94-SRNP-19, 5 Mar 94, ♂; 94-SRNP-20, ♀, ♀, X-4489; 94-SRNP-22, 31 Jan 94, ♀; 94-SRNP-25, 24 Jan 94, ♂; 94-SRNP-27, 11 Mar 94, ♂; 94-SRNP-29, ♀, ♂; 94-SRNP-31, 22 Feb 94, ♂; 94-SRNP-32, 5 Mar 94, ♂. Sector El Hacha, Vado Rio El Hacha, 290 m, 94-SRNP-879, 2 Jun 94, ♀; 94-SRNP-882, 11 Jul 94, ♂, X-4246. Sector Orosi, Estacion Maritza, 520 m, 95-SRNP-378, 14 Mar 95, ♂, X-4491. Sector Poco Sol, Poco Sol, 270 m, 91-SRNP-2737, 21 Feb 92, ♀; 92-SRNP-361, 20 Mar 92, ♂; 92-SRNP-379, 21 Mar 92, ♀; 92-SRNP-380, 5 Mar 92, ♀, X-4244; 92-SRNP-385, 27 Mar 92, ♀; 92-SRNP-386, 18 Apr 92, ♀; 92-SRNP-400, 21 Mar 92, ♀, X-4247; 92-SRNP-403, 23 Mar 92, ♂; 92-SRNP-410, 5 Mar 92, ♀; 92-SRNP-419, 14 Mar 92, ♀; 92-SRNP-426, 15 Apr 92, ♂; 92-SRNP-433, 10 Mar 92, ♂, X-4245; 92-SRNP-435, 21 Mar 92, ♂; 92-SRNP-437, 24 Mar 92, ♂; 92-SRNP-438, 15 Apr 92, ♀; 92-SRNP-441, 12 Mar 92, ♂, X-4487; 92-SRNP-444, 18 Mar 92, ♂; 92-SRNP-445, 29 Feb 92, ♂, X-3422; 92-SRNP-450, 18 Mar 92, ♀, X-4488; 92-SRNP-455, 15 Mar 92, ♀; 92-SRNP-458, 5 Apr 92, ♂; 92-SRNP-466, 30 Mar 92, ♂; 92-SRNP-470, 21 Apr 92, ♀; 92-SRNP-473, 5 Apr 92, ♀; 92-SRNP-477, 2 Mar 92, ♂, X-4278; 92-SRNP-480, 6 Mar 92, ♀, X-3423; 92-SRNP-498, 15 Apr 92, ♂; 92-SRNP-639, 29 Apr 92, ♀. Sector Poco Sol, Quebrada Aserradero, 160 m, 92-SRNP-354, 7 Apr 92, ♀; 92-SRNP-366, 13 Mar 92, ♂; 92-SRNP-370, 3 Mar 92, ♀; 92-SRNP-377, 23 Mar 92, ♂; 92-SRNP-698, 9 Jun 92, ♂; 94-SRNP-641, 8 May 94, ♂. Sector Santa Rosa, Cruz de Piedra, 290 m, 92-SRNP-345, 29 Feb 92, ♀. Sector Santa Rosa, Porton de Los Perros, 300 m, 94-SRNP-870, ♀, ♀, X-4490.

*Wild-caught paratype*: COSTA RICA, PROVINCIA GUANACASTE, Comelco, 8 km N Bagaces, 50 m, 24 May 1972, ♀, P. A. Opler (CAS).

**Etymology.** Named in honor of Dr. Hiroshi Kidono of the Japan International Cooperation Agency who is an enthusiastic and dedicated supporter of the INBio and ACG parataxonomists' research on the caterpillars of the Hesperidae of Costa Rica.

#### NATURAL HISTORY OF *DREPHTALYS KIDONOI* AND *DREPHTALYS ALCMON*

As stated above, just one adult of *D. kidonoi* has been collected in nature, although larvae have often been found eating both new and mature leaves of *Roupala montana* (Proteaceae), the only known host plant. This shrubby tree is abundant on the poor soils and rocky pastures in the central portion of the ACG at 100–500 m elevation (Figs. 31, 32). Since *R. montana* occurs throughout the dry forest remnants in Pacific coastal Mesoamerica, since it “ranges from Veracruz, Mexico, to Peru, Bolivia, and Brazil” (Burger 1983:14), and since adults of *D. kidonoi* elude collectors, we infer that this skipper is more widespread. In this connection, note that its sister species, *D. helixus*, is represented (a) in the USNM by 14 ♂ 1 ♀, all taken at a single, hilltop locality (Rodman) in the former Canal



Zone of Panama (on 12 different days in 5 different years), (b) in the AMNH by 1 ♂ from Balboa in the former Canal Zone of Panama, and (c) in the BMNH by 6 ♂, all from Panama (Evans 1952)—which suggests a geographically limited species. But it most certainly is not: Mielke, Miers, and Casagrande (Mielke pers. comm.) have caught 28 ♂ of *D. helixus* (only 1 or 2 on any given day, and always on hilltops) very far away in the southern Brazilian states of Santa Catarina (24 ♂ at Joinville) and São Paulo (3 ♂ at Morro do Diabo, Teodoro Sampaio) and in the city of Rio de Janeiro (1 ♂) (specimens in UFPR, 3 of them donated to USNM and examined by Burns); and C. Callaghan has caught 1 ♂ (on a hilltop at km 500 of the Belo Horizonte-Brasília highway) in Minas Gerais, the next Brazilian state to the north (specimen seen by Burns).

*Drephalys kidonoi* larvae (Figs. 21–23) are unlikely to be confused with any other hesperiid larvae known from the ACG. The dorsal and lateral part of the body is sharply, and rather narrowly, banded black on a whitish to greenish white background, while the head (which is slightly rugose) is pale to dark orange and devoid of markings. The black bands are broken by the whitish ground color just anterior to the spiracles on all segments but the first two and the last three. This banded color pattern starts to appear in the second instar; the first instar larva is green (once it has fed) with a black head. When the larva changes to a prepupa, the ground color becomes creamy, and the black bands, light beige (Fig. 23). The head may become lighter orange at this time.

*Drephalys alcmon* (Cramer) (Figs. 17–20), the only other species of *Drephalys* known from the ACG, ranges widely from Guatemala (1 ♀ from Cayuga in USNM) through Central and South America to Brazil and southeastern Peru (1 ♀ from 30 km SW Puerto Maldonado in USNM)—as well as the island of Trinidad (Cock 1984). Brazilian specimens come from northern and central states—Roraima: Ilha de Maraca, Alto Alegre (UFPR); Rondônia: Fazenda Rancho Grande, Cacaúlândia (Austin 1995, UFPR), Fazenda Urupa, Candeias do Jamari (UFPR); Pará (Evans 1952): Belém (Moss 1949), 15 km S Itaituba (USNM), Óbidos (UFPR), Santarém (UFPR); Mato Grosso: Alto Rio Arinos, Diamantino (USNM), Barra dos Bugres (UFPR), Fazenda Parana, Brasnorte (UFPR); Goiás: Goiás Velho (UFPR), Ilha do Bananal (UFPR); Pernambuco: Camaragibe, Recife (UFPR); and Espírito Santo: Linhares (UFPR). The latitude of the southernmost record (Linhares, Brazil, 19°25'S) is slightly higher than that of the northernmost record (Cayuga, Guatemala, 15°32'N). However, *D. alcmon*

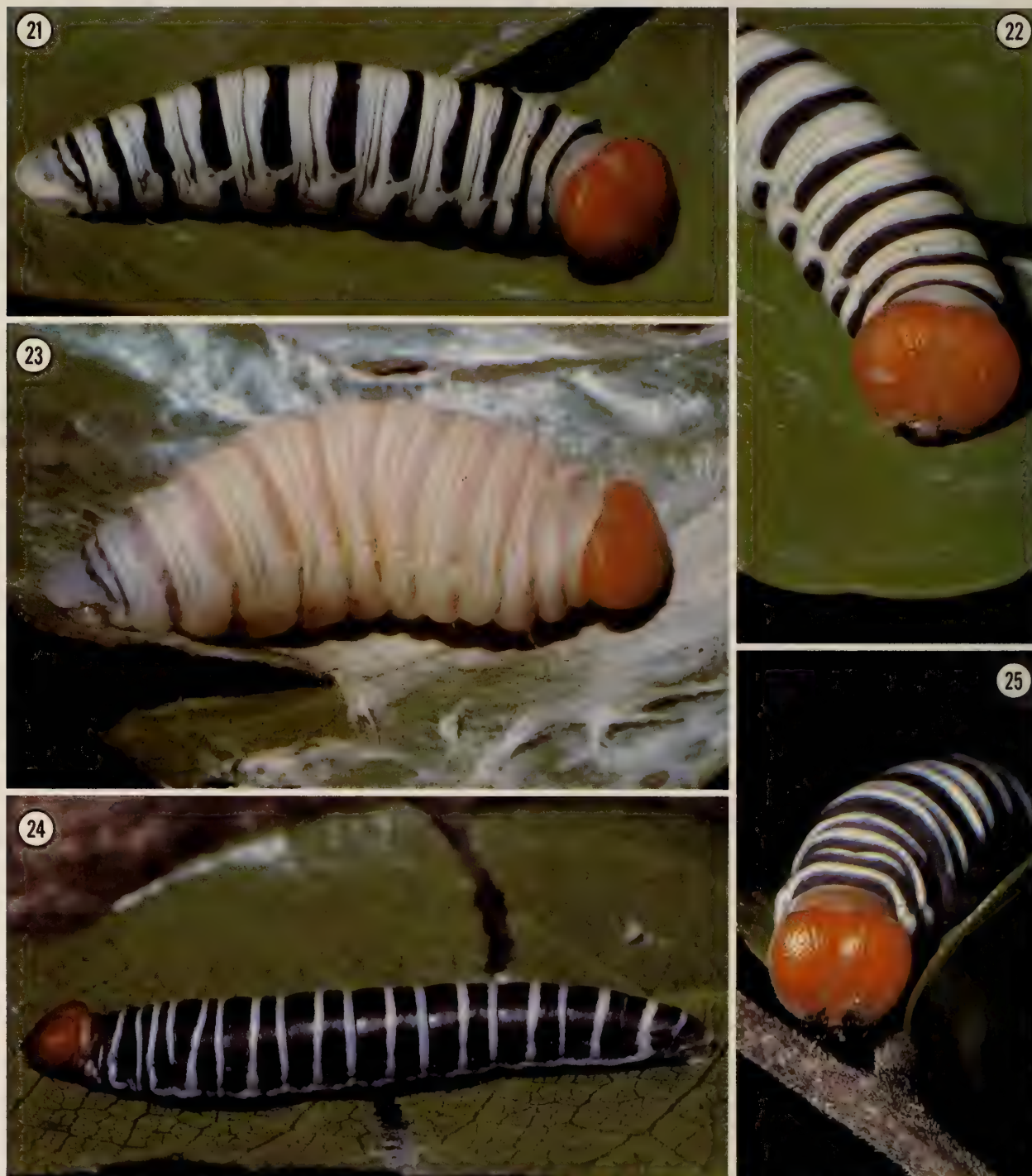
probably occurs as far north as southern Mexico (the distribution of its larval food plant would allow this—see below). When he recorded *D. alcmon* from Rondônia, Brazil, Austin (1995:127) gave for the rest of its range only “northeastern South America.” In his list of BMNH holdings, Evans (1952:27) included, besides specimens from the Guianas and Amazonian Brazil, “1 ♀ ‘Honduras’”; but the quotation marks were his way of questioning the accuracy of a locality label.

Adults of *D. alcmon* (Figs. 17–20) are superficially and morphologically well removed from the sister species *D. kidonoi* (Figs. 9–12) and *D. helixus* (Figs. 13–16). Although the larva of *D. alcmon* shares a general color pattern with that of *D. kidonoi*, its black bands are so broad that the white ground color is reduced to thin white bands connected to a thin, white ventrolateral line (Figs. 24, 25). Viewed from the front (Fig. 25), its orange (and slightly rugose) head bulges less than does that of *D. kidonoi* (Fig. 22).

The larvae of *D. kidonoi* (N = 236) apparently feed only on *Roupala montana* (Proteaceae). In the ACG, the larvae of *D. alcmon* (N = 70) apparently feed only on *Hirtella racemosa* Lamarck (Chrysobalanaceae) (Burns & Janzen in prep., Janzen & Hallwachs 1998), a quite unrelated plant—but a common one that spans the neotropics from central and southern Mexico to southeastern Peru, Bolivia, and northeastern São Paulo, Brazil (Prance & Campbell 1988, Prance 1989). In 1998, Aiello (pers. comm.) reared an adult male of *D. alcmon* from a larva found on *H. racemosa* in Loma del Río, Arraiján, Panama province, Panama (Aiello Lot 98-9). But in the vicinity of Belém, Pará, Brazil, Moss (1949:59) reared *D. alcmon* from larvae found on two food plants that were incompletely determined as “*Parinarium* or *Couepia*, *Rosaceae*.” “*Parinarium*” is presumably *Parinari*; and both *Parinari* and *Couepia* are now in the Chrysobalanaceae, along with *Hirtella*. Indeed, *Couepia* and *Hirtella* are sister genera, extremely closely related (Prance pers. comm.). Moss (1949:59) reared one other species of *Drephalys*, *D. eous* (Hewitson), whose “larval shelters [he] commonly observed in the forest on the leaves of . . . *Vochysia vismiaefolia* Spruce” (Vochysiaceae). So far (but admittedly it is not very far), different species of *Drephalys* seem to be specializing on food plants in taxonomically unallied families (Proteaceae, Chrysobalanaceae, and Vochysiaceae).

The drawings of last instar *Drephalys* larvae in Moss (1949:pl. I) are both black-and-white and small. Still, his *D. eous* larva (fig. 9) closely resembles our *D. kidonoi* larva (Figs. 21–23). However, his *D. alcmon* larva (fig. 11) is one in which every other vertical, thin, white band of ground color fails to reach the horizon—





FIGS. 21–25. Larvae of two species of *Drephalys* (*Drephalys*) from the Area de Conservacion Guanacaste, Guanacaste, COSTA RICA. **21**, *D. kidonoi* last instar larva in dorsolateral view (93-SRNP-8715, 11 January 1994). **22**, *D. kidonoi* last instar larva in anterior view (93-SRNP-8715, 11 January 1994). **23**, *D. kidonoi* prepupal larva in dorsolateral view (94-SRNP-147, 11 January 1994). **24**, *D. alcmon* penultimate instar larva in dorsolateral view (94-SRNP-8577, 10 October 1994). **25**, *D. alcmon* last instar larva in anterior view (96-SRNP-1091, 22 May 1996).

tal, thin, white ventrolateral line, something that happens only once, near the anterior end, in our examples of *D. alcmon* (Figs. 24, 25).

For both *D. eous* and *D. alcmon*, Moss (1949:59) notes that “the pupa squeaks audibly when touched.”

In all instars, the larva of *D. kidonoi* forms its shelter by silking together two halves of a leaflet (*R. montana* has pinnately compound leaves), thus folding the leaflet along its midrib so that its upper surface is inside the shelter. Search for larvae is greatly facilitated



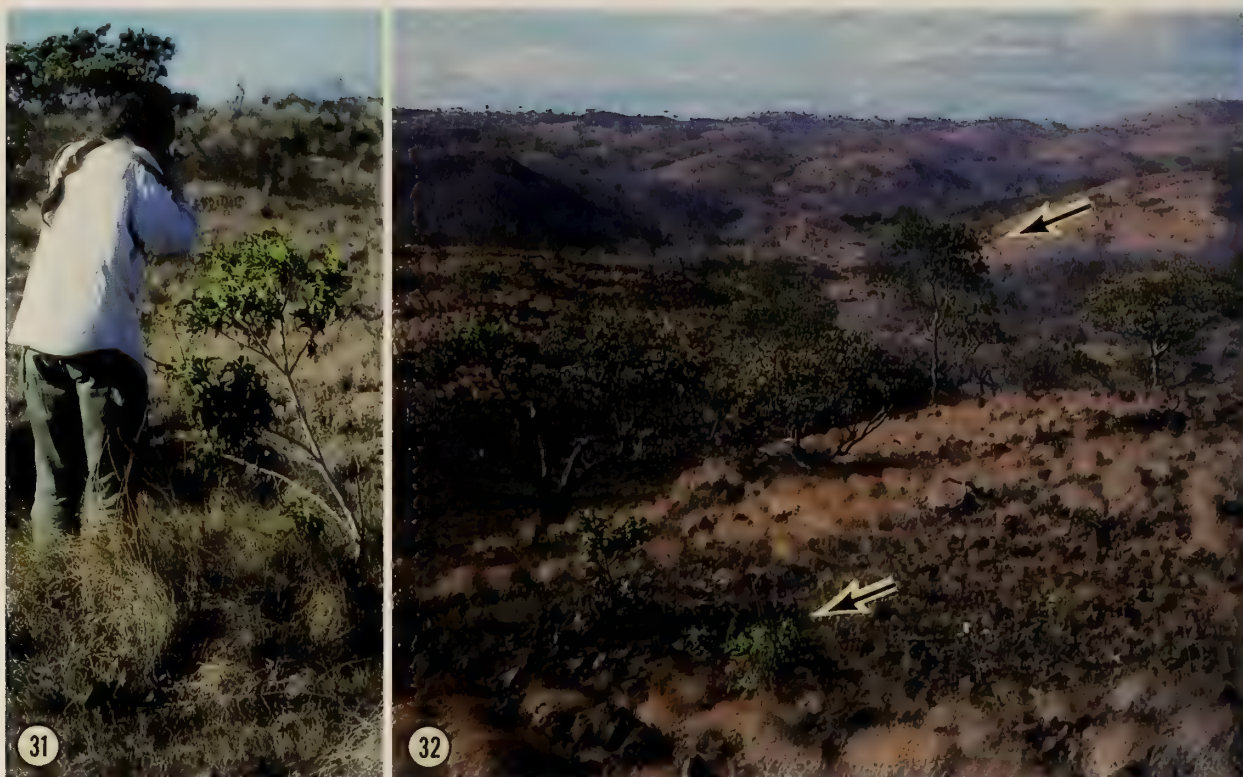
FIGS. 26–30. Pupae of two species of *Drephalys* (*Drephalys*) from the Area de Conservacion Guanacaste, Guanacaste, COSTA RICA. **26**, *D. kidonoi* in ventral view (93-SRNP-8708, 11 January 1994). **27**, *D. kidonoi* in lateral view (93-SRNP-8708, 11 January 1994). **28**, *D. kidonoi* in anterior view (93-SRNP-8708, 11 January 1994). **29**, *D. alcmon* in ventral view (96-SRNP-1090, 22 May 1996). **30**, *D. alcmon* in anterodorsal view (96-SRNP-1090, 22 May 1996).

by looking for shelters on young saplings and sucker shoots, where the folded leaflets are easier to see and where they may also be more abundant. However, the larvae are occasionally encountered at all heights above the ground and on leaves of all ages. The larva walks out of the shelter to feed at night and remains

within it by day. The larva of *D. alcmon* lightly silks together two leaves to form its shelter.

The pupa of *D. kidonoi* (Figs. 26–28) is largely ivory white. It has a pair of conspicuous pink/orange/brown-colored thoracic spiracles (false eyespots) and a black/brown “mustache” between the ivory-colored





FIGS. 31, 32. *Roupala montana* (Proteaceae)—larval food plant of *Drephalys* (*Drephalys*) *kidonoi*—in the Santa Elena Sector of the Area de Conservacion Guanacaste, Guanacaste, COSTA RICA, during the dry season. 31, Sapling (1 m tall) at the age commonly used as larval food (15 January 1986). 32, Sapling (lower arrow) and adult tree (upper arrow) in their general habitat (8 April 1985).

true eyes (Fig. 28). The true eyes turn red several days before eclosion and become dark brown the day before. The pupa of *D. alcmon* (Figs. 29, 30) is likewise ivory white with a pair of conspicuous pink/brown (false eye-like) thoracic spiracles, but it lacks the dark "mustache" (Fig. 30). The striking "face" on the anterior end of both species' pupae is part of a pupal defense against diurnal vertebrate predators that is commonplace in ACG hesperiids (Janzen in prep.).

The pupa of *D. kidonoi* rests in the whitish and densely silked pupation chamber that is constructed from the last larval shelter. The last instar larval skin remains in the pupal chamber and lodges close to the point where the cremaster attaches to the silked walls.

In captivity, the larva takes 45–55 days to develop from a newly-hatched first instar to prepupa. This puts *D. kidonoi* among the slower-growing pyrgine larvae that have been reared in the ACG (Janzen & Hallwachs 1998). Slowness of growth probably is related to feeding on leaves that range from newly expanded to very old and tough. The last instar larva remains 3–4 days in the prepupal stage and 16–18 days in the pupal stage. Such durations are normal for a pyrgine hesperiid of this body weight. There is no hint of prepupal

or pupal dormancy, either in the wet season or in the (very hot and dry) ACG dry season.

More than 90% of the 236 larvae collected between 1991 and 1997 were found in the first half of the ACG dry season (late December through March) (Janzen 1993). Four pupae were found in the wild in mid-February 1992, and adults eclosed from them a week later. However, a few larvae were also found in April, May, July, August, and November. It would appear that *D. kidonoi* breeds mainly during the first half of the dry season. At this time, almost all other species of Hesperidae that breed in this dry forest are sexually dormant adults on site, are dormant prepupae (very rarely), or have migrated out of these dry forests into nearby riparian bottomlands or the more distant evergreen, montane, cloud or rain forests to the east of the ACG dry forests.

The ACG habitat currently occupied by the food plant, *Roupala montana*, is extensive, deforested, windswept, highly insolated, and dry (Fig. 32). Most, if not all, of this habitat has been generated by centuries of logging and burning, which have left large areas as rocky plains and knolls with low, sparse, native grasses and three species of widely scattered, stunted, and rel-



atively fire-resistant trees: *Curatella americana* L. (Dilleniaceae), *Byrsonima crassifolia* (L.) DC (Malpighiaceae), and *Roupala montana* (Janzen 1988:fig. 26). In some of the old pastures, *R. montana* is the only species of tree present. All three of these fire-tolerant tree species are vertebrate-dispersed. Originally, the *D. kidonoi* population may well have persisted on a fragmented and low density *R. montana* population growing on cliff faces, ravine banks, and rocky outcrops scattered throughout the original old growth dry forest blanketing the ACG landscape.

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NEW PRONOPHILINE BUTTERFLIES FROM THE VENEZUELAN TEPUYES  
(NYMPHALIDAE: SATYRINAE)

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**ABSTRACT.** Four new species of satyrine butterflies collected in four Venezuelan tepuyes are described and illustrated: *Protopedaliodes ridouti* from the Roraima-Tepui, *Protopedaliodes profauna* and *Pedaliodes terramaris* from the Auyán-Tepui, and *Pedaliodes yutajeana* from the Cerros Yutajé, Yaví, and Marahuaka. Taxonomic considerations and discussion on affinities are presented.

**Additional key words:** Pantepui, *Pedaliodes*, Pleistocene, *Protopedaliodes*, Venezuela.

Venezuelan scientists involved in research on the tepuyes (most of them currently within national parks) have made major efforts to decrease and limit the so-called “ecological tourism” in this region. This is due mainly to their concern over the dramatic degradation of the fragile environments at the tops of these mountains. Propaganda recently generated by science fiction films (often recalling the imaginary Lost Worlds of Conan-Doyle and Crichton) and persons attempting to set new Guinness’ records in the tepuyes generate public clamor and still more visitor interest in the area. The accumulated result of such misguided publicity, together with the general paranoia about commercial collecting of wild animals and plants anywhere in the national territory, has resulted in the thoughtless enforcement of rigorous laws that virtually prohibit biological research in most of the Venezuelan protected areas.

Consequently, there is now an exceedingly complex bureaucracy to deal with in applying for insect collecting permits in the tepuyes (and elsewhere in Venezuela). Generally speaking, three separate applications must be prepared for the consideration and approval, respectively, of the National Council for Scientific and Technological Research (CONICIT), the National Parks Institute (INPARQUES), and finally the Service for the Fauna of the Ministry of Environment and Natural Resources (PROFAUNA). They have to be submitted synchronously and well in advance, taking into account the fact that the delivery of the third of these depends on the approval of the second, and so on. Even if these endless requirements were all satisfactorily met at the initial submission, we have found that there is no guarantee of receiving such permission, and when

given, permits are often so badly delayed that are out-of-date and useless.

To face this problem has become an essential worry for Venezuelan scientists (let alone foreigners), who find themselves handicapped in their field work, even if they are entirely innocent of any involvement with film and TV productions, or commercial dealing with biological specimens. As “illegal” procedures are being sternly punished with confiscation of material, financial penalties, and menace of imprisonment, it is rather frustrating to find that we are virtually forbidden to study our own biota while at the same time extensive gold mining (never controlled as are insect collecting activities) is quickly devastating large areas of pristine forests in marginal regions of the Venezuelan territory. These include all National Parks south of the Orinoco. Massive “ecotourism” and all its undesirable consequences however continues with no problems of permission (just a local application, approved on the day of submission) in the Canaima National Park and all of the tepuyes, even in the remotest Cerro de La Neblina.

This scenario leads us to believe that it will take several decades for Venezuelan and international scientists to be able to study good series of entomological samples from the tepuyes, which can satisfy the accepted paradigm of having two or more individuals to proceed to a satisfactory taxonomic description. In the meantime, we strongly feel that a few butterflies we know as undescribed, collected in four of the 54 tepuyes existing in Venezuela (all potentially populated by these insects), deserve to be described as part of a major revisionary work of the group currently being undertaken by the senior author. Two of these undescribed taxa are known from single male individuals. One is so distinctive within an endemic and hitherto monobasic genus (which was erected by ourselves in 1994) that we would not hesitate in providing a new place for it in the increasing list of Neotropical butter-

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fly names; the other one, although externally undistinguished, is also a new member of a small group of species which may be unmistakably recognized by the contortion of the tip of the male genitalic valvae.

Four descriptions are presented here. All type specimens, except for the solitary individual of *Protopedaliodes ridouti*, new species, which is held by The Natural History Museum (BMNH) in London, are deposited in the Museo del Instituto de Zoología Agrícola of the Universidad Central de Venezuela (MIZA) in Maracay, as required by the Venezuelan environmental authorities.

***Protopedaliodes ridouti* Vilorio & Pyrcz,  
new species  
(Figs. 1, 7)**

**Description.** *Male.* Forewing length: 30 mm ( $n = 1$ ). Eyes dark brown, hairy. Palpi twice as long as head, covered with long dark-brown hair. Antennae to over half costa. Thorax and abdomen all dark brown; walking legs (second pair) same length as in *P. kukenani* Vilorio & Pyrcz (third pair broken in holotype). Forewing subtriangular, apex and tornus obtuse, outer margin convex and smooth; hindwing oval, outer margin smooth. Upperside all dark brown, blackish in basal and postbasal areas; faint, barely visible ocellus in cell M1, black with white pupil. Underside forewing ground color dark brown, sparsely sprinkled with lighter brown or silvery scales on apex and upper one third of submarginal area; ocellus in cell M1 large, as wide as cell, black, pupilled with white, circled with faint orange framing. Hindwing ground color similar to forewing but liberally sprinkled with lighter brown scales over the entire surface; lighter area between postmedian and submarginal lines, forming a 5–8 mm wide band, being the narrowest in cell M2 and towards tornus on vein 1A (3 mm), its inner and outer edge do not merge; two large ocelli in cells R5 and Cu1, of same shape, color and size as on forewing. Genitalia illustrated in Fig. 7.

*Female.* So far unknown.

**Types.** *Holotype.* Male, Mt. Roraima, 8000 ft, Venezuela, 12-ix-1974, B. V. Ridout, B. M. 1974-650, BM(NH) Rhopalocera vial number 4198.

**Etymology.** We dedicate the name of this species to its collector, Dr. B. V. Ridout.

**Distribution.** This species is only known from the summit of the Roraima-Tepui (=Mount Roraima, Fig. 11), where it probably flies sympatrically with *Protopedaliodes kukenani*, and another pronophiline species (presumably of the genus *Lymanopoda* Westwood; Orellana, pers. comm.). For a description of the habitats, vegetation, and general geographic aspects of this region, see Brewer (1984).

***Protopedaliodes profauna* Vilorio & Pyrcz,  
new species  
(Figs. 2, 3, 8)**

**Description.** *Male.* Forewing length: 32–32.5 mm, mean = 32.25 ( $n = 2$ ). Eyes coffee brown, covered by short black hairs. Palpi twice as long as head, pale brown; outer ventral long hairs coffee brown, inner hairs shorter and light brown. Antennae reaching half of costa, black, except for ventral region of club, which is brown. Body dorsally coffee brown with very shiny hairs, ventrally pale brown, lighter towards abdomen, in general very hairy (including leg femorae), but hairs denser and shorter than on dorsal surface. Forewing triangular, apex and tornus slightly rounded, outer margin slightly convex; hindwing subtriangular, tornus somewhat truncated, outer margin moderately scalloped. Dorsal ground color of wings

dark coffee brown, very shiny; creamy-light brown scales between veins in fringes of both wings; brownish sheen on hindwing anal margin region; forewing exhibiting very thick androconial patches in discal region; hindwing very hairy on basal two thirds. Underside ground color of wings similar to upperside; lighter postdiscal bands on both wings, laterally limited (except near tornus) by darkening of ground color. Forewing band anteriorly broadened, dusted with reddish scales; sparse white scales on subapical and apical regions, more densely in inner border of band near costa; sparse short white hairs along costal region. Hindwing covered by short creamy-white setae, more densely towards basal region, anal margin, and on discal band; reddish scales dusted over basal region, in space anterior to cell. Genitalia in Fig. 8.

*Female.* Forewing length: 33.5 mm ( $n = 1$ ). The only known female is worn and differs from male in the following features: general color much paler; dorsal wing color rather paler towards distal third, particularly on forewing.

**Types.** *Holotype.* Male, Auyán-Tepui, 1700 m, Bolívar, Venezuela, 5°58'N, 62°32'W, 14/19-ii-1994, J. L. García, A. Chacón. *Paratypes.* 1 male same data; 1 female, Auyán-Tepui, 1800 m, Bolívar, Venezuela, 5°51'N, 62°35'W, 4/10-ii-1988, L. J. Joly & A. Chacón.

**Etymology.** This butterfly bears the name of one of the Venezuelan environmental institutions mentioned in the introduction. We do that because of the resulting euphony.

**Distribution.** Apparently endemic to the Auyán-Tepui (Fig. 11), an extensive table mountain massif in southeastern Venezuela. General accounts of the geography and ecological aspects of this region were presented by Brewer (1978) and Fundación Terramar (1993). *P. profauna* seems to fly in a different altitudinal zone located above the species described below.

***Pedaliodes terramaris* Vilorio & Pyrcz,  
new species  
(Figs. 4, 9)**

**Description.** *Male.* Forewing length: 27 mm ( $n = 1$ ). Eyes black, covered by short black hairs. Palpi twice as long as head, hairy, dorsally and ventrally black, laterally creamy-white. Body dorsally covered by dark, bright, brown hairs, ventrally pale brown (including hairs covering femorae), somewhat reddish on anterior part of thorax. Forewing triangular, apex and tornus softly rounded, outer margin more or less linear; hindwing suboval, outer margin excavated between veins. Wing upperside ground color chocolate brown, very dark in discal region (of both wings), lighter towards basal region and distal third, except in marginal region; hindwing also lighter in marginal region. Forewing upperside bearing six androconial patches in discal region, the two elongated ones in cell Cu2 not as distant as in *P. yutajeana*, new species. Wing underside groundcolor chocolate brown, postdiscal bands lighter, bordered distinctly but irregularly with darker lines that never reach tornus; marginal region reddish chestnut, flanked by fine dark chocolate brown lines on both sides; forewing basal third, region adjacent to costa, and inner margin, almost as light as postdiscal band; basal half of wing densely covered by short brownish hairs; some white scales over costal portion of band inner border; discal cell finely sprinkled with dark chocolate brown scales. Hindwing underside sprinkled with brown and reddish scales (the latter less conspicuous on postdiscal band), anal region suffused with brick-orange, and dusted with yellow scales; two submarginal white dots within band in cells Cu2 and M3, respectively; basal region very hairy. Genitalia illustrated in Fig. 9.

*Female.* So far unknown.

**Types.** *Holotype.* Male, Auyán-Tepui, 1500 m, Bolívar, Venezuela, 5°57'N, 62°39'W, 19/24-ii-1994, A. Chacón.

**Etymology.** The specific name, *terramaris*, is a derivation from the name of the Fundación Terramar, a private Venezuelan organization that has been responsible for much of the recent biological exploration of the tepuyes.

**Distribution.** Only known from the slopes of the Auyán-Tepui, where it flies in lower cloud forest.







***Pedaliodes yutajeana* Vilorio & Pyrcz,  
new species  
(Figs. 5, 6, 10)**

**Description.** *Male.* Forewing length: 29 mm ( $n = 1$ ). Eyes black covered by black hairs (with reddish sheen). Palpi twice as long as head, hairy, dorsally and ventrally black, laterally yellowish white. Antennae reaching approximately half of costa, dorsally dark brown, ventrally reddish. Thorax dorsally black, covered by very bright dark coffee hairs, as well as rest of body, ventrally lighter. Forewing triangular, apex and tornus slightly rounded, outer margin very softly sinuate; hindwing subtriangular, outer margin convex and moderately excavated between veins. Wing upperside ground color dark coffee brown, shiny, slightly lighter towards distal quarter (particularly in forewing), some light creamy-brown scales between veins in fringes; androconial patches on forewing discal region contiguous, two of them lengthened, and running parallel in cell Cu2. Wing underside ground color dark chocolate brown, lighter towards postmedial region. Forewing also lighter in basal quarter; some white scales dusted over costal region of band; reddish scales dusted over subapical region; six tiny submarginal white dots in cells R4 to Cu1; dense, short, reddish hairs on anterior portion of basal region. Hindwing postmedial band less distinct than on forewing; reddish suffusion in tornus and anal margin area; yellow scales dusted within band, from tornus along its inner margin, to costa; basal third of wing hairy; one submarginal white dot in cell Cu1, another one (vestigial) in M3; costal and marginal area with chestnut tone. Genitalia illustrated in Fig. 10.

*Female.* Forewing length: 30–32 mm, mean = 31 mm ( $n = 2$ ). In general bigger than male, with less bright coloration. Dorsally with light postdiscal bands, which on hindwing containing a suffusion of brick-reddish in costal region near apex. Ventral pattern similar to male, but ground color with general speckling of reddish chestnut scales (almost imperceptible within bands); marginal region reddish; forewing submarginal white dots variable, sometimes missing; hindwing exhibiting a contrasting “marble pattern” as a result of reddish and chocolate brown speckling over plain brown ground color; yellowish scales uniformly dusted over entire surface, especially concentrated in inner border of postdiscal band; series of five submarginal white dots in cells R5 to A2; anal region with reddish suffusion as in male.

**Types.** *Holotype.* Male, Cerro Marahuaka, 2470 m, Parque Nacional Duida-Marahuaka, Amazonas, Venezuela, 3°37'N, 65°22'W, 3/6-ii-1992, Exp[edición], Terramar, J. Clavijo, A. Chacón. *Paratypes.* 1 female, Cerro Yutajé, 1750 m, Amazonas, Venezuela, 5°45'N, 65°08'W, 12/17-ii-1995, J. Clavijo A., Exp[edición], Terramar; 1 female, Cerro Yaví, 2200 m, Amazonas, Venezuela, 5°43'N, 65°54'W, 24/28-ii-1995, J. L. García, Exp[edición], Terramar.

**Etymology.** The name of the species is derived from one of the original localities, the Cerro Yutajé.

**Distribution.** This species is distributed in an extensive, discontinuous, montane area of northern Amazonas State, from Cerro Yaví and Yutajé to Cerro Marahuaka (Fig. 11). This range implies that it may also be found in the intervening mountains: the Sierra de Maigualida, Jawa-Sarisariñama massif, and certainly the Cerros Huachamacari and Duida, which are adjacent to the Marahuaka. Geographical and ecological aspects of the area, as well as recent biological discoveries, are discussed by Michelangeli et al. (1988) and Fundación Terramar (1989, 1993).

## DISCUSSION

***Protopedaliodes.*** The genus *Protopedaliodes* was recently erected for a species (*P. kukenani* Vilorio & Pyrcz, 1994) from the upper cloud forest on neighboring table mountains in South-Eastern Venezuela, Kukenán-Tepui and Roraima-Tepui. Further research in 1995 in the Natural History Museum (BMNH) revealed the existence of a small collection of butterflies made by B. V. Ridout on the top of Mount Roraima. This material comprises 16 males and two females of *P. kukenani* (plus one male collected on the north ridge of Roraima, on the Guyana side, at 7400 ft., by Adrian Warren). This large series agrees with the original description of *P. kukenani* and no modifications of the specific diagnosis are required. However, among the Ridout material a single male was readily recognized to represent the second species of the genus (*P. ridouti*). In 1996 we examined the material recently collected on the tepuyes by staff members of the Museo del Instituto de Zoología Agrícola of the Universidad Central de Venezuela (MIZA), and found both *P. profauna* and the two species of *Pedaliodes* Butler also described in this paper. The above mentioned specimens of *Protopedaliodes*, plus the type series of *P. kukenani* (in MIZA) and five additional individuals of this species (three males, two females) obtained by the American mammalogist G. H. Tate in the summit of Roraima in 1927 (deposited in the American Museum of Natural History, New York [AMNH]), are to our knowledge the only ones existing in scientific collections.

*Protopedaliodes ridouti* is easily distinguished from its allies, *P. kukenani* and *P. profauna*, by its wing shape and quite different hindwing underside pattern, especially the well developed ocelli in cells R5 and Cu1. Although some specimens of *P. kukenani* also have faint ocelli in cell R5 of the underside of the forewing, in *P. ridouti* the ocelli are very well developed in forewing cell M1 and in cells R5 and Cu1 of the hindwing. The wing pattern of *P. ridouti* is unusual for pedalioidine butterflies, and is reminiscent, but perhaps not homologous to, that of the genus *Praepronophila* Forster (1964) (see also Miller 1986). It places *P. kukenani* well apart from other members of the tribe.

The type specimen of *P. ridouti* (30 mm) is slightly smaller than average sized *P. kukenani* (mean 32.8

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FIGS. 1–3. 1, *Protopedaliodes ridouti* Vilorio & Pyrcz, new species, *Holotype*. Male, Mt. Roraima, 8000 ft, Venezuela, 12-ix-1974, B. V. Ridout, B. M. 1974-650, BM(NH) Rhopalocera vial number 4198; right upperside, left underside. 2, *P. profauna* Vilorio & Pyrcz, new species, *Holotype*. Male, Auyán Tepui, 1700 m, Bolívar, Venezuela, 5°58'N, 62°32'W, 14/19-ii-1994, J. L. García, A. Chacón; right upperside, left underside. 3, *P. profauna* Vilorio & Pyrcz, new species. Female paratype, Auyán Tepui, 1800 m, Bolívar, Venezuela, 5°51'N, 62°35'W, 4/10-ii-1988, L. J. Joly & A. Chacón; right upperside (forewing discal white mark represents rubbing of the scales), left underside.







mm). Its wing shape differs, the hindwing apical and tornal corner being more angular and giving the wings of *P. ridouti* a slightly square appearance. Venation is the same for all three species of *Protopedaliodes*, but the wing fringes of *P. ridouti* are shorter.

The male genitalia of *P. ridouti* show certain very characteristic features common to this species and to *P. kukenani*, such as the extremely long, straight and toothed aedeagus, and the deep saccus. On the other hand, subunci are nearly atrophied in *P. ridouti*, its uncus is even longer than in *P. kukenani*, and its valvae are devoid of any secondary process. The wing pattern of *P. profauna* is simple and resembles *P. kukenani*. The genitalia of *P. profauna* is structurally characteristic of the genus, but the aedeagus is three times as broad as those of the two other species, and it lacks the tooth at the tip; the uncus is relatively short, thickened, and remarkably bifurcated at the extremity (so far a unique feature in the tribe it belongs to, the Pronophilini); the saccus is as deep as in the two other species, although curved downwards; the valvae resemble those of *P. kukenani*, but are more stylized.

Common features among the species of *Protopedaliodes*, such as the ground color of the upperside, the lack of any androconial patch on the forewing upperside, similar head and leg morphology, and the characteristic male genitalia, confirm the validity of the genus when compared to other American Pronophilini.

The existence of further species of *Protopedaliodes* in the Guayana shield area (one certainly sympatric with *P. kukenani*) directly implies that some radiation occurred within the Pantepui which, until the present time, has been poorly researched, as compared to avian or mammalian faunas or high altitude floras. The cloud forest fauna of the upper slopes of the table mountains in the Pantepui seems to be impoverished compared to similar montane habitats in the Andes. This is possibly due to the isolation of this region and relatively small area of suitable cloud forest habitats. Most butterfly species (including *Pedaliodes*, see below) reported to date from the cloud forests of the Pantepui are endemic, but apparently offshots of the Andean fauna (see Strand 1912, Brown 1932, Vitoria [1995], 1998, Vitoria & Pyrcz 1995, Pyrcz 1995, Neild 1996), at least in those cases where affinities of the species can be recognized.

*Protopedaliodes* cannot yet be related with certainty to any pronophilines known from the Andes. We previously suggested that it has possible affinities with the less derived lineage of *Pedaliodes* (*sensu lato*) (i.e., *Praepronophila*, *Parapedaliodes* Forster). This assumption was based, among other characters, on male genitalic morphology (which is also reminiscent of that of *Praepronophila*).

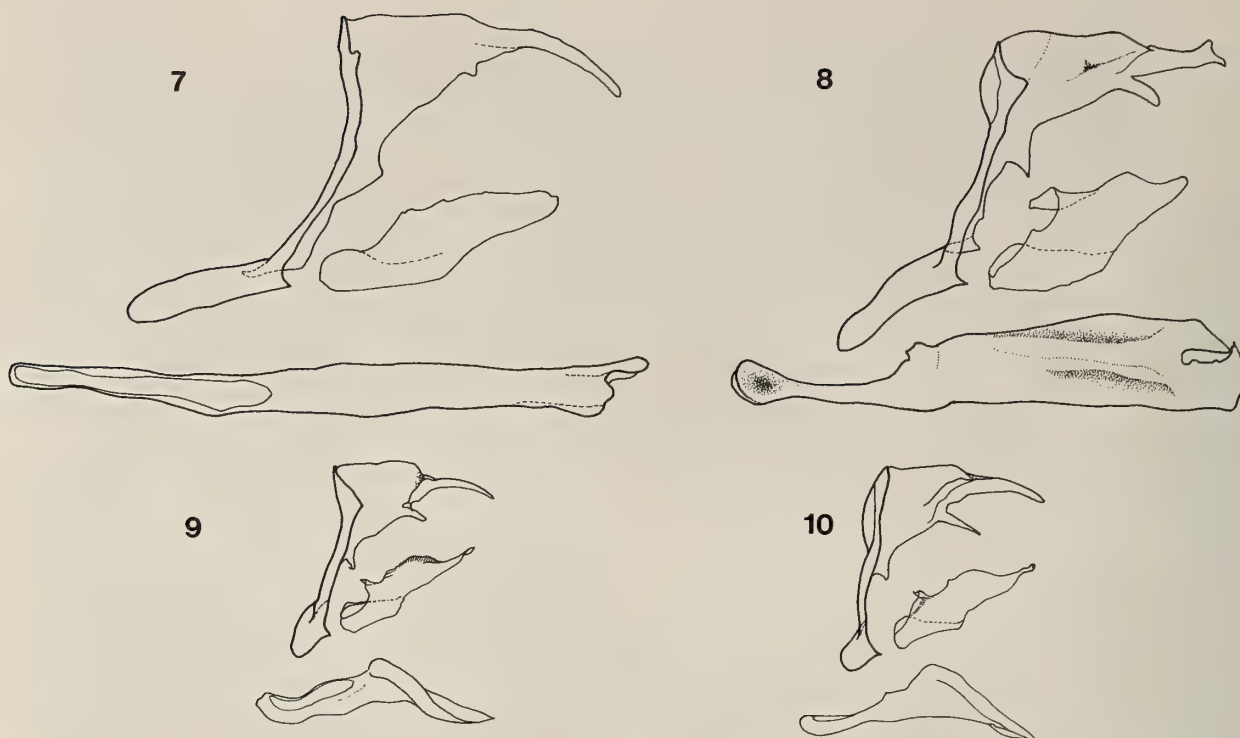
It seems unlikely that *Protopedaliodes* originated from modern Andean "colonizers", and we favor the hypothesis that it is derived from older elements proper to the Pantepui. A fast adaptive radiation of *Protopedaliodes* could also be involved as a factor obscuring its phyletic origins.

***Pedaliodes*.** *Pedaliodes* Butler *sensu stricto* is certainly one of the most speciose genera of Satyrinae in the world. We recognize 132 described valid species plus nine subspecies, and 105 species (excluding the two described here) plus 22 subspecies confidently identified as new, undescribed taxa, which are deposited in seven major entomological collections in America and Europe (Vitoria unpubl.). This makes a grand total of 270 taxa, most of which are highly endemic to restricted montane areas of the tropical Andes. Only 15 species are known to occur out of the Andes, five of them being restricted to the mountains of the Pantepui (i.e., *P. roraimae* Strand, 1912 (Gran Sabana, Roraima-Tepui and Kukenán-Tepui, 1280–1900 m), *P. demarmelsi* Vitoria, [1995] (Cerro de La Neblina, 1690–2100 m), *P. chaconi* Vitoria, 1998 (Serranía de Tapirapécó, 1300 m), *P. terramaris* (Auyán-Tepui, 1500 m), and *P. yutajeana* (tepuyes of northern Amazonas State, from Cerro Yaví to Cerro Duida, 1750–2470 m)). Other alleged records from the Guayana region, such as *Pedaliodes prytanis* (Hewitson) (Adams & Bernard 1979:109) and *P. manis* (C. & R. Felder) (d'Abrera 1988:852), are incorrect. The first one is based on two old specimens mislabelled as being from Corosita, Caura Valley (in the BMNH), which were purchased by J. J. Joicey from Klages. This is obviously wrong as *P. prytanis* is endemic to the highest elevations of the Cordillera de La Costa, where Klages obtained part of his collections. The second case represents misidentifications of four males of *P. roraimae* (from Mount Roraima, Venezuela) in the same institution.

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 FIGS. 4–6 4, *Pedaliodes terramaris* Vitoria & Pyrcz, new species, *Holotype*. Male, Auyán Tepui, 1500 m, Bolívar, Venezuela, 5°57'N, 62°39'W, 19/24-ii-1994, A. Chacón; right upperside, left underside. 5, *P. yutajeana* Vitoria & Pyrcz, new species, *Holotype*. Male, Cerro Marahuaka, 2470 m, Parque Nacional Duida-Marahuaka, Amazonas, Venezuela, 3°37'N, 65°22'W, 3/6-ii-1992, Exp. Terramar, J. Clavijo, A. Chacón; right upperside, left underside. 6, *P. yutajeana* Vitoria & Pyrcz, new species, Female paratype, Cerro Yutajé, 1750 m, Amazonas, Venezuela, 5°45'N, 65°08'W, 12/17-ii-1995, J. Clavijo A., Exp. Terramar; right upperside, left underside.





FIGS. 7–10. Male genitalia of the species herein described; in each case aedeagus and left valva have been removed from natural positions. 7, *Protapedaliodes ridouti*. 8, *P. profauna*. 9, *Pedaliodes terramaris*. 10, *P. yutajeana*.

The species of *Pedaliodes* found south of the Orinoco River are all closely related, as deduced by the strong similarities in wing pattern and genitalia. With the exception of *P. demarmelsi* (which exhibits a very distinctive color pattern), they are, in fact, almost indistinguishable from each other in facies. *Pedaliodes terramaris* and *P. yutajeana*, however, can be told apart by subtle differences in size and wing shape (compare Figs. 4 and 5), and by the differences in the distribution of the male androconial patch on forewing cell Cu2 (see descriptions above). The shape and extent of the male forewing scent patches have proved to be most useful in identifying *Pedaliodes* species with few wing markings, and using these characters we have been able to recognize seven “black” species occurring sympatrically in the Colombian Cordillera Occidental (Pyrce & Vilorio 1999b), all previously misidentified under one or two names (Adams 1986).

When compared, the valvae of *P. roraimae* and *P. chaconi* are shorter and more robust than those of *P. terramaris* and *P. yutajeana*. Differences between *P. roraimae* and *P. chaconi* were discussed in a previous publication (Vilorio 1998).

The Pantepuian *Pedaliodes* belong to a group that is not restricted to the Guayana biogeographical region. On the contrary, this is the most widely distributed

clade within the genus, ranging from Mexico to Bolivia (see below). Vilorio [1995] pointed out the structural and superficial similarities between the Pantepuian *P. demarmelsi*, and the Mesoamerican species *P. dejecta* (Bates) and *P. napaea* (Bates). This observation was at that time surprising, because of the apparently huge distributional gap between Mesoamerica and the Cerro de La Neblina, especially for these montane insects. However, a better understanding of the morphology, taxonomy, and distribution of a number of closely related species that occur at lower altitudinal levels (the lowest possible for the genus) in the cloud forest of almost every mountain range in between these range extremes has led us to believe that the group probably started diverging in isolation only geologically very recently, perhaps from a single widespread lowland ancestor.

Although Neotropical cloud forest satyrines are exceedingly sedentary and do not migrate (De Marmels et al. 1996, Vilorio et al. in prep.), it is possible that past global climatic fluctuations may have led to the lowering and conjugation of cloud forests, enabling the ancestor of these butterflies to spread between currently isolated cloud forest “islands.”

Results of paleoclimatic studies in Venezuela (Rull 1996) and other areas of the northern Neotropics

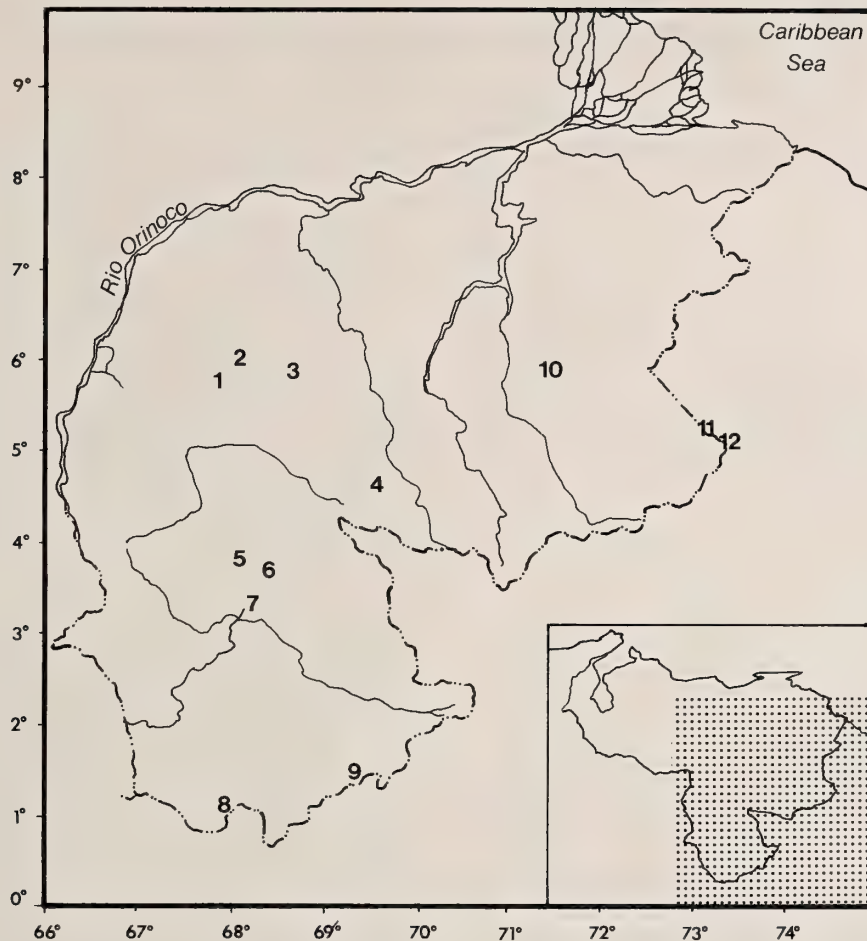


FIG. 11. Localities of the Pantepui region mentioned in the text: 1, Cerro Yutajé. 2, Cerro Yaví. 3, Sierra de Maigualida. 4, Jaua-Sarisariñama massif. 5, Cerro Huachamacari. 6, Cerro Marahuaka. 7, Cerro Duida. 8, Cerro de La Neblina. 9, Serranía de Tapirapecó. 10, Auyán-Tepui. 11, Kunénán-Tepui. 12, Roraima-Tepui (modified from Steyermark 1986, Fundación Terramar 1993 and Huber 1995).

(Schubert 1987), indicate much lower average temperatures at the end of the Pleistocene, and although conditions were also much drier in some areas, this does not rule out the possibility that the floristic equivalent of cloud forest could have been present in others. We speculate that not only the Pantepuiian *Pedaliodes*, but also all allied congeners<sup>1</sup> elsewhere in the Neotropics, may be derived from an ancestor which was widespread at lower elevations during the Pleistocene.

<sup>1</sup> The members of this group of allied congeners outside the Pantepui are: *Pedaliodes croizatorum*. Viloria and Camacho (Serranía del Turimikire, northeastern Venezuela, 1500–2300 m); *P. pisonia* (Hewitson) (Venezuelan Cordillera de La Costa, 1100–1700 m); *P. manneja* Thieme (Cordillera de La Costa and Sierra de Perijá, 1800–2300 m); *P. montana* Adams & Bernard (Andes from Venezuelan Cordillera de Mérida to Bolivian Yungas, 1050–3000 m); *P. ereiba* (C. & R. Felder) (Cordillera Oriental, Colombia, ca. 1800 m); *Pedaliodes canela* (= *Pedaliodes canela*) Pyrcz and Viloria (Cordillera Occidental, Colombia, 1000–3300 m); *P. phrasiclea* Grose-Smith (Andes of Colombia to Bolivia, 1000–2250 m); *P. pomponia* (Hewitson) (Andes of southeastern Ecuador, 450–1400 m); *Pedaliodes balnearia* Pyrcz and Viloria (1999a)

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(southeastern Ecuador, 2000–2600 m); *Pedaliodes*, new species (Zamora valley, 1000–1300 m); *Pedaliodes*, new species, Lamas & Viloria, MS (southern Ecuador to northern Bolivia, 1800–2300 m); *P. phrasiclea* Grose-Smith (Andes of southern Peru and Bolivia, 750–3000 m); *P. prosa* Staudinger (southeastern Peru and Bolivia, 1000–3000 m); *P. dejecta* Bates (mountains of Panama, Costa Rica and Guatemala, 850–2300 m); *P. cremera* Godman & Salvin (Irazú volcano, Costa Rica, ca. 2000 m); *P. napaea* Bates (mountains of Guatemala and southern Mexico [Chiapas], 1000–1700 m); *P. circumducta* Thieme (Mexico, 1100–1450 m); *Pedaliodes* sp. [nov.] Luis-Martínez and Llorente (1993) (Mexico, Puerto Los Mazos, Jalisco, Michoacán Mountains and Sierra de Atoyac in Guerrero, ca. 1000–2000 m).



study is based on. Our gratitude is also expressed to J. M. González (Fundación Terramar) for successfully locating the Tate collection of Venezuelan satyrines in the AMNH. The junior author acknowledges A. Mee and A. Neild for their hospitality in London, for their company and for editing preliminary manuscript notes. This research has been supported by The British Council, CONICIT, and La Universidad del Zulia (PhD grant to ALV), and the Institute of Zoology of the Jagiellonian University (internal grant DS/IZ 1995/01, to TWP).

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## AN EXAMINATION OF INTRASEASONAL VARIATION IN THE INCIDENCE OF MELANISM IN PEPPERED MOTHS, *BISTON BETULARIA* (GEOMETRIDAE)

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**ABSTRACT.** We examined daily catch records of peppered moths (*Biston betularia*) taken over a forty-year period to determine whether melanic and pale forms of this species fly at the same or different times within seasons. We also compared the emergence rates of the two forms from reared broods to determine whether differences in developmental rates might contribute to intraseasonal flight patterns. Although melanic phenotypes develop slightly faster than their typical siblings in some laboratory broods, the field records show no consistent pattern for one phenotype being more common than the other early or late in the same summer. The work is discussed in the context of industrial melanism for which this species is the classic example.

**Additional key words:** *cognataria*, f. *carbonaria*, industrial melanism, f. *swettaria*.

Industrial melanism is a familiar textbook example of observable evolution brought about by natural selection. The term pertains to increases in the frequencies of genetically determined melanic versus pale phenotypes in populations living in habitats modified by regional industrial development and urbanization. The phenomenon has been well documented in many species of Lepidoptera; however, attention has focused primarily on the peppered moth, *Biston betularia* (L.) (Geometridae). The broad aspects of the subject have been reviewed recently by Majerus (1998), Sargent et al. (1998), and Grant (1999).

The corpus of experimental work to date is consistent with the interpretation that selective predation on the moths by birds is the primary, though not exclusive, force driving the changes in the frequencies of peppered moth phenotypes (Majerus 1998). Kettlewell (1955, 1956) provided the first quantitative evidence that birds eat the different color phases of peppered moths according to their conspicuousness on different backgrounds. His mark-release-recapture experiments also demonstrated that the melanic phenotypes fared better than the pale forms in soot-blackened woodlands; whereas, the pale forms fared better than the melanics in unpolluted woodlands.

Kettlewell (1973) entertained other possibilities beside selective predation that might contribute, at least in part, to the high incidence of melanism in moth populations living in the vicinities of British industrial centers. He speculated that larvae developing in the early part of the summer feed on leaves that are less contaminated by industrial pollutants than are the older leaves that larvae feed on later in the summer.

From his observations of larval developmental rates, he proposed that pale peppered moths, as fast developers, avoided pollution, and/or that the melanics, as slow developers, "may be capable of getting rid of toxic substances." He cited no reference to support his statement that "slow feeding and a capacity for excreting noxious materials has been demonstrated . . . outside the Lepidoptera" (Kettlewell 1973:85).

Unfortunately, Kettlewell's developmental analysis of peppered moths was limited to one brood that was partially consumed by mice, and a second brood that provided "no corroboration of the earlier results." He also acknowledged that he could provide no evidence from samples of wild populations that industrial melanic forms change in frequency during the flight period within single seasons. However, he did discuss intraseasonal changes in phenotype frequencies for several other moth species which show what he called "ancient" (=stable polymorphism) melanism. For example, pale *Amathes glareosa* increase late in the season (the melanics appear early on); whereas, *Cleora repandata* melanics increase, relative to pale forms, as the season progresses.

In analyses of seasonal catch records of other moth species polymorphic for melanic forms, Bishop et al. (1978) concluded that melanic *Gonodontis bidentata* emerged later than pale forms, and Sargent (1983) reported slight increases in melanism during the second half of seasons in *Phigalia titea*. As only field data were available from these studies, clear distinctions between selection on the adults and developmental differences in emergence schedules between the phenotypes were not possible. Equally problematical, S. Poitout (cited



TABLE 1. June (=A) and July (=B) catch records of *B. betularia* phenotypes (Mel. = melanics, T+I = typicals and f. *insularia*) at Caldy Common between 1959 through 1998. The phenotypic distributions during June and July of each year are compared by G-tests of independence.

Year	Mel	T+I	G	Year	Mel	T+I	G	Year	Mel	T+I	G	Year	Mel	T+I	G
59A	174	15		69A	349	25		79A	387	111		89A	52	114	
59B	90	4	1.46	69B	216	20	0.67	79B	111	23	1.72	89B	13	40	0.91
60A	178	11		70A	658	68		80A	379	115		90A	36	68	
60B	34	2	—	70B	112	10	0.18	80B	103	40	1.30	90B	15	35	0.33
61A	161	18		71A	109	8		81A	118	46		91A	102	337	
61B	240	12	4.45*	71B	79	11	1.75	81B	178	65	0.08	91B	139	355	2.93
62A	159	17		72A	45	3		82A	43	15		92A	227	750	
62B	588	38	2.56	72B	202	26	1.26	82B	45	19	0.22	92B	32	111	0.05
63A	725	67		73A	102	14		83A	219	111		93A	41	146	
63B	185	18	0.03	73B	181	21	0.21	83B	226	133	0.88	93B	22	65	0.37
64A	238	25		74A	99	14		84A	172	105		94A	39	196	
64B	335	37	0.03	74B	178	22	0.14	84B	43	32	0.56	94B	26	87	2.01
65A	361	40		75A	78	16		85A	189	144		95A	33	149	
65B	70	7	0.06	75B	155	20	1.60	85B	271	256	2.34	95B	13	66	0.11
66A	163	18		76A	129	29		86A	213	198		96A	5	78	
66B	110	8	0.93	76B	242	46	0.05	86B	169	225	6.78**	96B	12	106	1.12
67A	123	10		77A	68	12		87A	141	201		97A	12	165	
67B	243	21	0.02	77B	360	50	0.46	87B	41	61	0.03	97B	5	56	—
68A	209	26		78A	91	28		88A	44	66		98A	14	113	
68B	216	26	0.01	78B	205	31	5.92*	88B	29	40	0.07	98B	12	87	0.07

\*p < 0.05

\*\*p < 0.01

by Bishop et al. 1978) showed in laboratory strains of *Spodoptera exigua* that melanic genotypes had a longer total development than non-melanic genotypes; thus melanic individuals tended to emerge from pupae later than the non-melanics, but no field data were reported.

The above studies serve to illustrate that generalities are not obvious regarding developmental differences and/or in intraseasonal variations in flight patterns between melanic and pale forms of polymorphic moth species. Therefore, we have analyzed the flight patterns in *B. betularia* directly, and compared the emergence rates of melanic and pale phenotypes. To determine if melanic and pale phenotypes fly at different times during the summer, we examined the daily catch records of peppered moths taken at a single location over a forty-year period. To assess potential differences in emergence schedules, we recorded the eclosion sequences of melanic and pale phenotypes from three large broods produced from controlled crosses.

#### MATERIALS AND METHODS

##### Field studies of intraseasonal flight patterns.

*Biston betularia* were collected near Caldy Common,

West Kirby, England over a period of 40 years, beginning in 1959. The original purpose of the study was to assess frequency changes in the melanic, pale, and intermediate phenotypes over the course of years; these annual changes have been reported elsewhere (see Clarke et al. 1985, 1994, Grant et al. 1996, 1998). To determine if the different phenotypes fly at different times during the same season, we reexamined the daily catch records for each of the 40 years moths were trapped at this location.

Each season a mercury vapor (MV) light trap was operated nightly from 1 June through 31 July. When virgin females were available, an assembling (pheromone) trap was also used. No difference in the proportions of the phenotypes caught by one trapping method or the other has ever been observed (Clarke et al. 1994), but the incidental use of the assembling trap does increase the total catch size. For our analysis, therefore, we subdivided each season into early and late halves based on calendar date (June versus July) rather than by the mid-point (median) of the total numbers of the moths caught within seasons. We then tabulated the numbers of each phenotype caught during the first and second halves of each season. The null

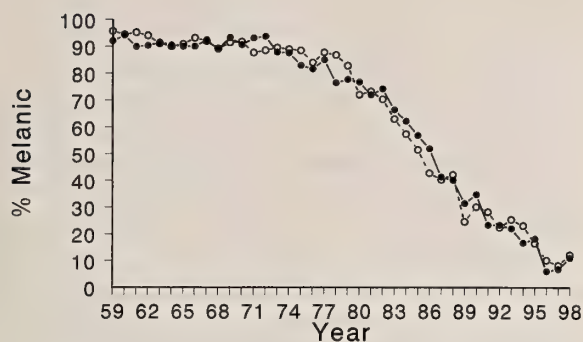


FIG. 1. The decline in the frequency of melanic *B. betularia* between 1959 through 1998 at Caldy Common, West Kirby, England, plotted from June samples (solid symbols) and from July samples (open symbols).

hypothesis is that there should be no difference in the percentage of melanics caught in the early and in the late samples taken during the same summer.

**Laboratory experiments on differential emergence.** To determine if differential emergence (time to eclosion) of melanic versus pale phenotypes exists, we crossed known heterozygous melanic *B. betularia cognataria* to their pale siblings. (The expected ratio of pales to melanics among the progeny from such matings is 1:1.) The stock material was produced by a melanic female crossed to a pale male, both of which were caught at the same location in Pennsylvania in 1996, and the crosses used in our experiments were made using their progeny which emerged in the spring of 1997.

In all, three sets of siblings were crossed, and their broods were subdivided to avoid overcrowding. The caterpillars were housed inside plastic "garbage cans" and were provided a continuous supply of fresh leaves from a single, large Chiswell crab apple tree (*Malus* spp.). The caterpillars pupated "at will" in moistened beddings in the bottoms of their containers. The pupae were then stored in containers lined with moistened paper towels. All storage containers were checked daily to remove newly emerged adults until the experiment was terminated several weeks after emergences ceased entirely and no living pupae remained. For each brood, each moth to emerge was identified by phenotype and sex and the date of its emergence.

## RESULTS

**Field studies.** From 1959 through 1998, 18,255 *Biston betularia* were collected near Caldy Common.

The year-to-year sample sizes varied widely, ranging between 122 to 1120, with an average annual catch of  $456 \pm 257$ . The early and late halves (June vs. July) of seasons also varied widely with respect to sample sizes, with mean catches at  $259 \pm 206$  and  $197 \pm 143$ , respectively. The differences between the early and late sample sizes, though large, are not statistically significant by paired samples *t*-tests ( $t = 1.622$ ,  $df = 39$ ,  $p = 0.113$ ), nor by the non-parametric Wilcoxon's signed-ranks test ( $p = 0.226$ ).

The complete set of catch records, subdivided by early (A = June) and late (B = July) catches, are summarized by phenotype in Table 1. In the table, the melanics (*f. carbonaria*) are separated from the other phenotypes (pale = *f. typica* or "typicals" and intermediates = *f. insularia*). The intermediates have remained rare at Caldy Common (for complete data through 1993 see Clarke et al. 1994), therefore the combined category (T+I) is essentially "typical" (pale), or non-melanic.

Sample sizes permitting, the numbers of melanics and non-melanics collected during the first half and second half of each season were compared using  $2 \times 2$  contingency *G*-tests of independence. The *G* statistics are listed in Table 1. Of the 38 comparisons made, only three showed significant differences in the phenotypic proportions between the early and late halves of the same season; in two instances the melanics increased significantly ( $p < 0.05$ ) in the second half of the season, and in one instance the melanics declined very significantly ( $p < 0.01$ ) during the second half of the season. In 35 of the 38 comparisons, no significant differences in the proportions of melanics between the early and late subsamples within seasons were observed.

To test for the possibility that small but consistent differences might exist within seasons (differences too slight to be detected by *G*-tests), we analyzed the entire 40-year record by Wilcoxon's signed-ranks test. The null hypothesis is that the differences in the percentages of melanics collected during first and second halves of seasons are random. The data show that the percentage of melanics increased during the second half of summers 23 times, and decreased 17 times (Fig. 1), but the differences are not significant by Wilcoxon's signed-ranks test ( $p = 0.55$ ).

Between 1977 and 1997 the annual incidence of melanism declined rapidly at Caldy Common (Fig. 1), and for several years during this same period, there appeared to be a short run of seasons in which the percentage of melanics decreased in the second half of summers compared to the first half. However, the pattern is not consistent throughout the period of rapid annual decline in melanism, and the differences in



TABLE 2. Early and late emergences from reared broods of *B. betularia cognataria* from crosses expected to produce 1:1 ratios of melanic and pale (typical) phenotypes. The phenotypic distributions between the early and late groups within each brood are compared by G-tests of independence.

Brood		Melanics	Typicals	G
A	Early	53	46	0.31
	Late	49	36	
B	Early	30	23	4.37*
	Late	16	29	
C	Early	27	27	0.47
	Late	23	30	

\*\* $p < 0.05$

melanic frequencies between first and second halves of seasons are not significant by Wilcoxon's signed-ranks test ( $p = 0.82$ ).

**Differential emergence.** We recorded the emergence date, sex and phenotypes of all adults produced by the three crosses of heterozygous melanics mated to their pale, homozygous siblings. Eclosion patterns within broods generally begin with one or a few adults emerging from puparia on the initial day, then the number of daily emergences increases quickly and peaks a few days later, after which the daily emergences tail off until finally many days may separate the stragglers from the main group and from each other. The null hypothesis of our experiment is that the difference in emergence sequence within broods is not related to the color phenotypes; therefore, the proportions of melanics and typicals should be the same in the first half of a brood to emerge as in the second half.

We divided each brood into early and late groups using the median. All of the moths emerging up to and including the day the first half of the total emergences for the brood was reached were assigned to the early group, and all of the moths emerging after that day were assigned to the late group. Table 2 lists the early and late emergences by phenotype (melanic and typical) for each of the three broods. The numbers of melanics and typicals emerging during the early and late periods are compared within broods by  $2 \times 2$  contingency G-tests of independence. The G statistics are also listed in the table. In brood B, melanics are significantly more common in the early than in the late group ( $p < 0.05$ ), but no significant emergence differences are apparent in the other two broods.

#### DISCUSSION

The data from Caldys Common provide little support for the idea that the different phenotypes of *Biston betularia* fly at different times of the season. That three of the 38 contingency tests indicated significant

intraseasonal differences between the phenotypic proportions is consistent with type-I error rates expected when large numbers of statistical comparisons are made (Sokal & Rohlf 1981). Furthermore, only two of the three observed significant deviations from random expectations were skewed in the same direction which further supports that these exceptional years can be attributed to chance. Of these three exceptional years (1961, 1978, 1986), only 1986 shows a very pronounced deviation in phenotypic proportions between the early and late halves of a season, and in this instance the significant decline in the proportion of melanics occurred during the brief run of intraseasonal declines in melanism that occurred during those years of the steepest declines in the annual incidence of melanism. Here, at least, it seems reasonable to suggest that selection at the adult stage rather than developmental differences in emergence schedules might account for the drop in melanism within that season.

Differences in emergence schedules between melanic and pale peppered moths are slight, at best. Of the three broods we examined, only one showed significantly accelerated emergence of the melanics versus their typical siblings. Different broods, no doubt, emerge throughout the normal season of several months, and if developmental differences, however slight, between melanics and pale forms are consistent, then, in the absence of offsetting selection at the adult stage, we should expect to observe a consistent bias favoring melanics earlier in the summer. Clearly this did not happen over the 40 years of observations at Caldys Common.

Our developmental studies in the laboratory employed the North American subspecies, *B. betularia cognataria*, and our field studies centered on the British subspecies of peppered moths, *B. betularia betularia*. Direct comparisons between the two must be qualified. American "pale" or typical forms are generally much darker than British typicals; however, the melanics (called f. *carbonaria* in Britain and f. *swettaria* in America) are phenotypically indistinguishable, and are caused by alleles at the same locus (Grant & Clarke in prep.). The melanics, both in America and Britain, have also shown parallel increases (Owen 1962) and decreases (Grant et al. 1995, 1996) in frequencies associated with environmental modifications related to industrial development and urbanization. The reductions in melanism on both continents are now widespread (Grant et al. 1998).

The phylogenetic relationship (Rindge 1975, Clarke et al. 1993), and the genetics of melanism in these subspecies (West 1977, Grant & Clarke in prep.), and the

ecological events coincidental to the parallel evolutionary changes in phenotype frequencies (Grant et al. 1996, 1998) combine to suggest that we are observing the same basic phenomenon in peppered moth populations on both sides of the Atlantic. While we must remain cautious in extrapolating what we learn from the study of one subspecies to draw conclusions about the other, we also recognize that what we learn from one subspecies might be instructive in our study of the other. In this instance, there again appears to be agreement: No consistent intraseasonal flight pattern differences between pale and melanic British peppered moths are apparent, nor are the differences in emergence schedules of pale and melanic American peppered moths consistent among broods.

Our study does not address one of Kettlewell's (1973) suggestions that differences in developmental rates might exist among the larvae of different genotypes that produce pale and melanic adult phenotypes. No clear relationship between emergence rates between melanic and pale peppered moths and the time the forms spend as larvae has ever been established; therefore, our study on emergence sequences does not bear directly on the question of the seasonal conditions early and late larvae might experience. However, there is evidence that *B. betularia cognataria* is bivoltine (Owen 1962, Manley 1981); therefore, larvae of those genotypes producing melanic and pale adults in the first versus the second generations of summers must endure late and early summer conditions, respectively, as they feed and develop. Yet, there is no evidence that the proportions of melanic and pale adults change consistently between the first and second broods of summers (Owen 1962, Manley 1981). These observations do not support Kettlewell's speculations that selection at the larval stage influences melanism at the adult stage.

We do not consider this a "negative results" paper. There has been much speculation about the relevant ecological factors and the putative selective agents responsible for industrial melanism, and now its decline (recently critiqued by Majerus 1998, Sargent et al. 1998, and Grant 1999). The occasional but recurring query that intraseasonal variation in the frequencies of the forms may offer some insights can, in our view, be laid to rest. Part of the process in identifying what is important from what is not involves the process of elimination. We hope we are making progress.

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## URIC ACID DEPOSITION IN LARVAL INTEGUMENT OF BLACK SWALLOWTAILS AND SPECULATION ON ITS POSSIBLE FUNCTIONS

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**ABSTRACT.** From the first through third instar, larvae of the black swallowtail, *Papilio polyxenes* Fabr., display a distinctive color pattern characterized by an irregular circle of white pigment on the dorsum. This white spot is surrounded by brown pigmentation, creating the impression of a bird dropping. It has long been assumed that this color pattern evolved as a defense mechanism against avian predators. We report here that the source of the white color is accumulated uric acid. Although uric acid has traditionally been viewed as an excretory product, it also can act in biological systems as a powerful antioxidant. Thus, the possibility exists that the white spot serves a protective function not only against predators in a high fidelity mimicry system, but also against oxidative stress generated by the phototoxic allelochemicals that characterize most hostplants of *Papilio* species.

**Additional key words:** *Papilio polyxenes*, bird dropping, furanocoumarin.

Early instars of a range of Lepidoptera species are brownish in color with a white saddle traversing the middle of the abdomen; this color pattern, from the human perspective, bears a remarkable resemblance to a bird dropping and thus has been characterized as an example of homotypism, or protective resemblance to an object considered inedible by a predator (Edmunds 1974). Although this pattern has been reported in at least one nymphalid genus (and typifies the larvae of the viceroy *Basilarchia archippus archippus* (Cramer), the red-spotted purple *Basilarchia arthemis astyanax* (Fabr.), and the white admiral *Basilarchia arthemis arthemis* (Drury)), it is practically universal among early stages of species in the genus *Papilio* (Lepidoptera: Papilionidae) (Munroe 1961).

Among the many substances contributing to larval lepidopteran pigmentation patterns is uric acid. Although uric acid is the major nitrogenous waste product of terrestrial insects (Cochran 1985), in many species it is retained and deposited in body tissue. This mechanism of dealing with excess nitrogen is known as storage excretion (Wigglesworth 1942, 1965, 1987) and provides a source of pigmentation, particularly in larval stages. Mauchamp and Lafont (1975) demonstrated that most of the uric acid in young *Pieris brassicae* (L.) caterpillars lies in the integument and is accumulated in the fat body before pupation, and Buckner and Newman (1990) determined that uric acid deposition in the integument is principally responsible for the appearance of white stripes that contrast with the green abdominal base color. Uric acid, presumably generated by larval metabolism, also can be found as a pigment in the yellow scales of *Papilio xuthus* L. (Tojo & Yushima 1972) and in the wings of male *Pieris brassicae* (Lafont & Penetier 1975).

In that birds are uricotelic, producing uric acid as the principal form of waste nitrogen, the white color of bird droppings is due to the presence of uric acid. We examined the integument of larvae of *Papilio polyxenes* Fabr., the black swallowtail butterfly, a species that displays the typical *Papilio* early stage "bird dropping" morphology, in order to determine if in fact the white saddle results from the accumulation of uric acid, the substance that provides the model for the mimetic resemblance. We also examined the integument of ultimate (fifth) instars, to determine if uric acid contributes to color patterns in mature larvae as well, and in adult male butterflies, to ascertain whether sequestered uric acid is retained through metamorphosis.

### MATERIALS AND METHODS

The eastern black swallowtail butterfly, *Papilio polyxenes asterius* Stoll., is found throughout eastern North America, ranging from southern Canada to Florida; it also occurs west along the eastern Rockies into northern Mexico (Opler and Krizek 1984). The larval stages feed almost entirely on herbaceous representatives of the families Apiaceae and, to a more limited extent, Rutaceae, and are found in a variety of open habitats. Larval development requires from two to three weeks, depending on temperature and host-plant (Blau 1981). Larvae in the first three stadia are primarily black, with a characteristic white saddle across the dorsal midsection; fourth and fifth instars are greenish-white to green, with black bands running horizontally across each segment, interrupted by a series of yellow to orange spots (Fig. 1). In central Illinois, there are two to three generations each year. Principal natural enemies of the black swallowtail in-



FIG. 1. Third (left) and fifth (right) instar *Papilio polyxenes* caterpillars.

clude spiders, wasps, predaceous bugs in the families Nabidae, Reduviidae, Coreidae, and Pentatomidae (Blau 1981, Feeny et al. 1985), ants, and possibly birds. Caterpillars defend themselves with an eversible osmeterial gland, the constituents of which change developmentally from primarily mono- and sesqui-terpenes in early instars to aliphatic acids and their esters in fourth and fifth instars (Berenbaum et al. 1992).

Gravid female *P. polyxenes* were collected in Champaign County, Illinois, and allowed to oviposit on foliage of parsley, *Petroselinum crispum* (Mill.); eggs collected in this manner were used to found a colony from which larvae were taken for experimental use. Caterpillars were reared on potted parsley or on parsnip, *Pastinaca sativa* L., plants in a greenhouse at 27°C (day); 21°C (night) under a 16L:8D photoperiod. As caterpillars reached either third or fifth instar, they were collected for chemical analysis. Male adults collected earlier from a laboratory colony initiated with wild-caught butterflies from Champaign County, Illinois, were stored at -80°C prior to chemical analysis.

Prior to all larval tissue collections, we removed the gut and Malpighian tubules. Epidermis of the abdomen of the third instar was divided into portions corresponding to the white saddle area and the remaining brown portion; each portion was analyzed separately. The final instar was divided according to apparent integument coloration. Black bands, green ground color, and yellow spots were cut out with iridectomy scissors and analyzed separately. The wings of the males were divided into black parts and yellow spots by cutting out the spots and each tissue type was analyzed separately. All tissues were collected directly into dry ice-chilled microcentrifuge tubes (1.8 ml) and kept in a freezer at -80°C prior to the uric acid assay.

We homogenized tissue samples with a tissue tearor (Biospec Products, Inc., Bartlesville, Oklahoma) and used a chloroform rinse to free the solution of lipophilic compounds. The integument was eluted in lithium carbonate (1%) to dissolve uric acid and after centrifugation (12,200 g) an aliquot of the supernatant was used for uric acid determination (Van Handel 1975). Each aliquot was brought up to a volume of 2 ml with distilled water. To each sample we added 1 ml of reagent (copper sulfate 0.05%, glycine 1.6%, sodium carbonate 4%) and 0.05 ml neocuproine reagent (Sigma, St. Louis, Missouri). Optical density was determined at 450 nm wavelength (Perkin Elmer Lambda 3B spectrophotometer). Because ascorbic acid can interfere in the uric acid assay (25 µg shows the same optical density as 0.9 µg uric acid), we corrected uric acid readings according to the ascorbic acid content of the sample (Omaye et al. 1979). To quantify ascorbic acid, 0.5 ml of supernatant was added to 0.5 ml of ice-cold 10% trichloroacetic acid, mixed thoroughly, and centrifuged for 5 minutes (12,200 g); 0.5 ml of supernatant was mixed with 0.1 ml of DTC (thiourea,  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ , 2,4-dinitrophenylhydrazine in 9N  $\text{H}_2\text{SO}_4$ ; Omaye et al. 1979) and incubated for 3 hours at 37°C, to form the 2, 4-dinitrophenylhydrazone. After incubation, the test tube was removed from the water bath and placed into ice water; 0.75 ml of ice-cold  $\text{H}_2\text{SO}_4$  (65%) was added and the solution mixed well. Solutions stood at room temperature for 30 more minutes, after which time we measured the absorbance at 520 nm.

## RESULTS AND DISCUSSION

Integument from ten third instars and nine fifth instars and wing scales from three adult male butterflies were analyzed for their uric acid content and distribution. All parts of the integument of third instar *P. polyxenes* contain measurable amounts of uric acid (Table 1). The white saddle, however, contains over



TABLE 1. Distribution of uric acid in the variously colored integuments of third and fifth instar and male wings of *Papilio polyxenes*. Values are given as the mean (standard deviation).

Life stage	N	Integument color	Uric acid (g/mg)
Third	10	Brown	57.2 (16.1)
Third	10	White	116.0 (57.6) <sup>a</sup>
Fifth	9	Black	24.9 (6.9)
Fifth	9	Green	49.1 (20.3) <sup>b</sup>
Fifth	9	Yellow	45.5 (9.2) <sup>c</sup>
Male	3	Black	2.2 (0.5)
Male	3	Yellow	15.0 (2.5) <sup>d</sup>

<sup>a</sup> Significantly different from brown integument, paired  $t = 3.72$ ,  $p = 0.005$

<sup>b</sup> Significantly different from black integument, paired  $t = 3.2$ ,  $p = 0.013$

<sup>c</sup> Significantly different from black integument, paired  $t = 5.7$ ,  $p = 0.0001$

<sup>d</sup> Significantly different from black scales, paired  $t = 8.6$ ,  $p = 0.01$

twice the amount of uric acid in brown-colored integument (paired  $t$  test,  $t = 3.72$ ,  $p = 0.005$ ). Integument that appears light in color in fifth instars also contains significantly greater amounts of uric acid than does adjacent integument that is black in color. Yellow spots contain almost twice as much uric acid ( $t = 5.65$ ,  $p = 0.0001$ ) as black stripes; the green ground color also contains almost twice the uric acid content of the black stripes ( $t = 3.19$ ,  $p = 0.013$ ). The accumulation of uric acid in the yellow wing scales in male butterflies is sevenfold higher than the amount of uric acid in the black wing scales ( $t = 8.6$ ,  $p = 0.01$ ). Over all life stages examined, uric acid content is highest in the white saddle of the third instar.

To a large extent, caterpillars rely on coloration to avoid visually orienting natural enemies. Although some species rely on crypsis (matching their background) and concealment, many can remain in plain sight by virtue of aposematism and associated unpalatability or by mimetic resemblance to inedible objects or substances. Birds have been identified as important predators of caterpillars in general (Morris 1972, Holmes et al. 1979, Atlegrim 1989, Marquis & Whelan 1994) and the body coloration of many species is thought to reflect selection pressures exerted by avian predation. Resemblance to a bird dropping may be common in that it is likely such a color pattern would be unappetizing to a wide variety of birds. In *P. polyxenes*, the appearance of the white saddle of the "bird dropping" pattern is largely due to the accumulation of uric acid, the same substance that creates the white, shiny appearance of authentic bird droppings. The fidelity of the visual mimetic resemblance to a bird dropping is no doubt enhanced by use of a substance identical to that found in the "model."

Resemblance to a bird dropping is at least in part responsible for the ability of early stage *P. polyxenes* to forage in full view of predators. Such foraging is ad-

vantageous in that caterpillars can process food more quickly and efficiently at higher temperatures associated with daylight hours (Ali et al. 1990). Such behavior, however, is not without attendant risks. Exposure to sunlight (particularly ultraviolet wavelengths) can cause oxidative stress; this stress may be exacerbated by the presence of photosensitizing allelochemicals in foliage. The apiaceous hosts of *P. polyxenes* (indeed, of most *Papilio* species—Berenbaum 1983) characteristically possess furanocoumarins, photosensitizers that can cause oxidative damage to DNA (Berenbaum 1991). Although all stages of *P. polyxenes* are capable of rapid and efficient metabolism of these compounds (Harrison et al. submitted), early instars in general have higher relative consumption rates than late instars (Slansky & Scriber 1985) and thus may encounter greater quantities of furanocoumarins relative to their body weight. While melanin in the dark parts of *P. polyxenes* integument may function as a neutral density filter, eliminating photoactivating wavelengths, the white saddle could potentially leave caterpillars vulnerable to ultraviolet light exposure.

Uric acid may be selectively retained by *P. polyxenes*, and *Papilio* species in general, not only because of its color but because of its powerful antioxidant and radical-scavenging properties (Becker 1993). The function of uric acid as an antioxidant in insects has already been established. Souza et al. (1997) observed greatly increased urate concentrations in the hemolymph of *Rhodnius prolixus* following a blood meal and suggested an antioxidant protective function of urate against prooxidant activity generated during the hydrolysis of hemoglobin. In *Drosophila melanogaster*, the antioxidant properties of urate have been demonstrated by the sensitivity of urate-null mutants to experimentally induced oxidative stress (Hilliker et al. 1992). The role of uric acid in epidermis as a protective pigment has also been suggested. In *Anopheles* mosquito larvae, the white dorsal pigmentation may represent protective coloration against solar radiation. Anopheline larvae are confined to shoal biotopes, living at the air/water interface and lying horizontally immediately below the water surface. Under these circumstances, the antioxidant properties of uric acid could effectively reduce possible damage by UV radiation (Benedict et al. 1996). Other antioxidants (particularly antioxidant enzymes) are known to occur in the integument of swallowtails (Lee and Berenbaum 1992), and foliage of swallowtail hostplants has been demonstrated to produce singlet oxygen at the leaf surface (Berenbaum and Larson 1988), which may present particular risks to integumentary tissues.

Thus, the high concentrations of uric acid in the

white saddle of the "bird dropping" morph of young black swallowtail caterpillars may serve multiple purposes—contributing to a compelling mimetic/protective resemblance to an inedible object in the environment while at the same time scavenging free radicals generated by ultraviolet light exposure and ingestion of photosensitizers. Such physiological economy may be enhanced further by the fact that accumulation of uric acid, a waste product generated as a consequence of processing food, does not divert nitrogen away from other physiological needs, as would synthesis of such nitrogenous pigments as pteridines or ommochromes.

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## FEEDING PREFERENCE OF *HELICONIUS ERATO* (LEP.: NYMPHALIDAE) IN RELATION TO LEAF AGE AND CONSEQUENCES FOR LARVAL PERFORMANCE

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**ABSTRACT.** In South Brazil, female *Heliconius erato phyllis* (Fabricius) lay isolated eggs on branch tips of *Passiflora suberosa* Linnaeus, leading to early larvae first contacting young host plant tissues. These feed on young tissues, but the adaptive meaning, if any, for such an association is still unknown. In this paper, we determine what leaf ages are usually consumed by each instar, the existence of feeding preference in relation to leaf age, and the performance of *H. erato* when fed either on young or old leaves of *P. suberosa* under laboratory conditions. Freshly-hatched larvae were transferred to the terminal portion of isolated, intact shoots, and observed daily for order of leaf choice until pupation. Feeding preference in relation to leaf age was evaluated for all instars through choice tests using leaf disks from young and mature leaves. Additionally to evaluate induction of feeding preference, larvae were reared through fourth instar on either young or mature leaves and then tested using the same choice procedure. Growth performance was assessed by progressively transferring larvae, according to instar number, from intact shoots to sections where apical portion was cut off. Larvae fed starting at the terminal bud (young tissues) and moving progressively to lower leaves of increasing age (mature leaves). Larvae of all instars consumed more young leaf disks, and preference for old leaves could not be induced. Larvae reared initially on young tissues had greater survivorship and grew faster than those on mature, and this may explain the oviposition site selection and larval feeding preference of this butterfly.

**Additional key words:** host-plant selection, heliconian butterflies, passion vines, leaf age effects.

*Heliconius erato phyllis* (Fabricius) (Nymphalidae) is common in the forests of southern Brazil (Brown & Mielke 1972). It uses a number of passion vine species as larval hosts, a few being preferred in a given locality (Benson et al. 1976, Brown 1979, 1981, Ramos & Freitas 1999). Isolated eggs are laid primarily on terminal buds of *Passiflora* shoots, young tendrils and young leaves (Benson 1978, Perico 1995, Mugrabi-Oliveira & Moreira 1996a). Larvae feed initially on young leaves near the apical portion of shoots (Alexander 1961, Benson 1978). Ovipositing females reject shoots deprived of or with a damaged apical portion, and prefer to lay on large shoots compared to small (Mugrabi-Oliveira & Moreira 1996a). They also assess egg- and larval-load, and reduce daily oviposition rates under low host-plant availability (Mugrabi-Oliveira & Moreira 1996b).

There are at least three hypotheses to explain *Heliconius* oviposition and early larval feeding on young *Passiflora* tissue, which are not necessarily mutually exclusive. First, Benson et al. (1976) suggested that *Heliconius* oviposition on passion vine tendrils would help to prevent egg-predation, because eggs on tendrils are less likely to be attacked by ants. In addition, Benson (1978) hypothesized that the feeding pattern of heliconian larvae that use young tender growth, such as *H. erato*, was in part shaped by interspecific competition with species specialized on older leaves. Also, it is known that host-plant selection by phytophagous insects is linked to plant suitability as larval food (Jones 1991, Bernays & Chapman 1994). Thus, it is expected that *H. erato phyllis* oviposition on the api-

cal portion of host-plants is also related to higher suitability of the corresponding tissues as larval food.

In this paper, we address the latter hypothesis from a behavioral ecology perspective. Feeding of *H. erato phyllis* larvae and its consequences are evaluated regarding variation in leaf age on shoots of *Passiflora* (*Plectostemma*) *suberosa*. This widely spread passion vine is a primary host of *H. erato phyllis*, and one of the most abundant passion vine species in southern Brazil (Menna-Barreto & Araújo 1985, Perico & Araújo 1991, Perico 1995). Information on the phenology of *P. suberosa* and corresponding effects on *H. erato phyllis* oviposition site selection are provided by Mugrabi-Oliveira & Moreira (1996a). Specific goals of the current study are 1) to characterize the natural feeding pattern of *H. erato phyllis* larval instars in relation to *P. suberosa* leaf age, 2) to evaluate the feeding preference of each instar regarding leaf age, and 3) to determine the consequences of feeding on leaves of variable age on survivorship, growth rate and adult size.

### MATERIALS AND METHODS

**Insects and plants.** Larvae used in the experiments came from eggs obtained from an *H. erato phyllis* outdoor insectary maintained at the Zoology Department of Federal University of Rio Grande do Sul, Porto Alegre, RS (see Mugrabi-Oliveira & Moreira 1996a). *P. suberosa* plants were obtained from cuttings that were transplanted into plastic pots. The plants originated from a population at Aguas Belas Experimental Station, Viamão County. The plastic pots were provided with 50 cm high wooden frame support for shoot growth, covered with a fine mesh cloth and maintained in an outdoor screened cage. Prior to the

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tests, plants were standardized for size by removing all branches except the main shoot in each pot. Experiments were conducted in a large laboratory chamber, adopting the prevailing abiotic conditions for the region during the summer (photoperiod 14L:10D, temperature  $25 \pm 1^\circ\text{C}$ , humidity  $75 \pm 5\%$ ).

**Feeding pattern.** To determine larval feeding pattern in relation to leaf age, twenty freshly hatched *H. erato phyllis* larvae were individually placed on the terminal bud of healthy growing shoots bearing 12 open leaves. Additional studies that have been carried out in our laboratory (S. S. Borges & G. R. P. Moreira unpubl. data) showed that in all cases when young larvae are put on any mature leaf, they move to the tip of *P. suberosa* shoots, always starting feeding on the terminal bud. Larvae were inspected for molting daily until pupation. At each inspection, we noted the age of leaf being consumed. To make sure that molts were not overlooked, larvae were gently marked with small colored dots of enamel paint (Testors) on the dorsal part of the penultimate abdominal segment. Leaf age was determined by leaf position in relation to the terminal bud (made up of apical meristem, leaf primordia and unopen leaves) (Fig. 1A).

**Choice experiments.** Feeding preference in relation to leaf age was evaluated through leaf disk choice tests. Trials were conducted in plastic pots, following the methodology described in Hanson (1983). The same twenty larvae were used over all instars; corresponding rearing procedure followed that described above. Unless noted, two leaf age categories were adopted: young (consisting of the first and second open leaves on actively growing branch) and mature (sixth and seventh open leaves). Disks were cut with a cork borer (diameter of 6.75 mm;  $35.78 \text{ mm}^2$  in area), and a fixed number offered (3, 3, 6, 12 or 18 disks of each age per larvae tested from first to fifth instar, respectively). Young leaf disks alternated with mature ones in the pot. To keep leaf disks from drying out, pots were covered with a plastic film. Leaves were collected from different plants every time. Total leaf area offered a given instar was adjusted to double the average leaf area consumed by a given instar in 5 hours (C. A. Barcellos & G. R. P. Moreira unpubl. data). All trials lasted for 5 hours, after which larvae were returned to their original rearing plants.

To evaluate possible induction of feeding preference in relation to leaf age, additional 40 larvae were reared up to third instar on young leaves. After molting to fourth instar, half of them were transferred to cuttings containing only mature leaves; the remaining 20 larvae were kept on cuttings bearing young leaves. They were all then individually tested in the fifth instar

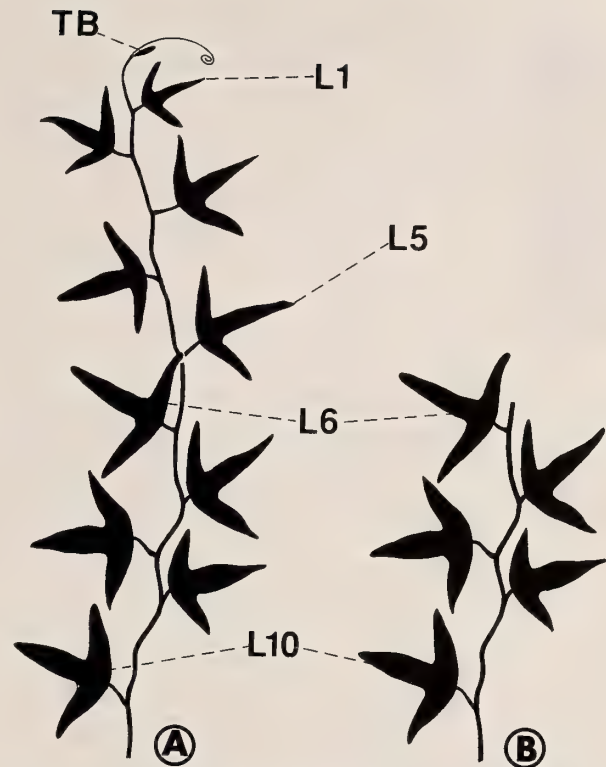


FIG. 1. Schematic representation of *Passiflora suberosa* shoots used to determine influence of leaf age on *Heliconius erato* larval performance. **A**, intact, with terminal bud and ten open leaves; **B**, lower section, with five mature leaves (terminal bud and five apical open leaves were cut out). **TB**, terminal bud; **L**, open leaf. Numbers indicate position in relation to shoot apex. Tendrils and stipules associated with open leaves were not drawn.

using the leaf-disk choice test described above (18 disks of each age per larvae).

Feeding was measured as area of disk eaten, recorded by placing the disks against graph paper at the end of each feeding trial and counting the number of square millimeters corresponding to the missing leaf area. If only young leaves were damaged, or over twice the area of young as mature leaves was consumed, larvae were scored as having discriminated in favour of young leaves. Conversely, if only mature leaves were consumed, or over twice the area of mature as young leaves was missing, then larvae were scored as having chosen mature leaves. Feeding trials were recorded as neutral when neither leaf-age category had more than twice the damage of the other (see Thomas 1987). To test the hypothesis that consumption of young leaves was greater than mature, scores were tested using one-tailed sign tests, following the procedure described in Conover (1980).

**Larval performance and adult size.** To determine leaf age effects on performance, larvae were in-



TABLE 1. Experimental scheme adopted to test influence of *Passiflora suberosa* leaf age on *Heliconius erato* larval performance. Treatments correspond to numbers of instar staying on intact shoots.

Treatment	Shoot type offered as food	
	Intact	Lower section
0		all instars
1	instar I	instars II-V
2	instars I and II	instars III-V
3	instars I-III	instars IV and V
4	instars I-IV	instar V
5	all instars	

dividually reared on potted plants receiving one of the following shoot types: 1) intact, with ten leaves and terminal bud; 2) lower section, with five mature leaves (terminal bud and five apical open leaves were cut out)

(Fig. 1). Six different treatments were used. Larvae were transferred from plants with intact shoots (type 1) to those with mature leaves (shoot type 2) according to instar completion (Table 1). For example: "In treatment 0, larvae were placed directly on shoots with mature leaves; in treatment 5, larvae were allowed to complete all five instars on intact shoots". A completely randomized block design was adopted; the experiment was carried out ten times (dates = block effect), one replicate per treatment was conducted on each occasion. Since there was no block effect, data were treated within an one-way design (10 replicates per treatment). Larvae were checked daily for molting until death, or up to emergence to the adult stage. Forewing length of freshly emerged adults was measured with callipers. Data from development rates

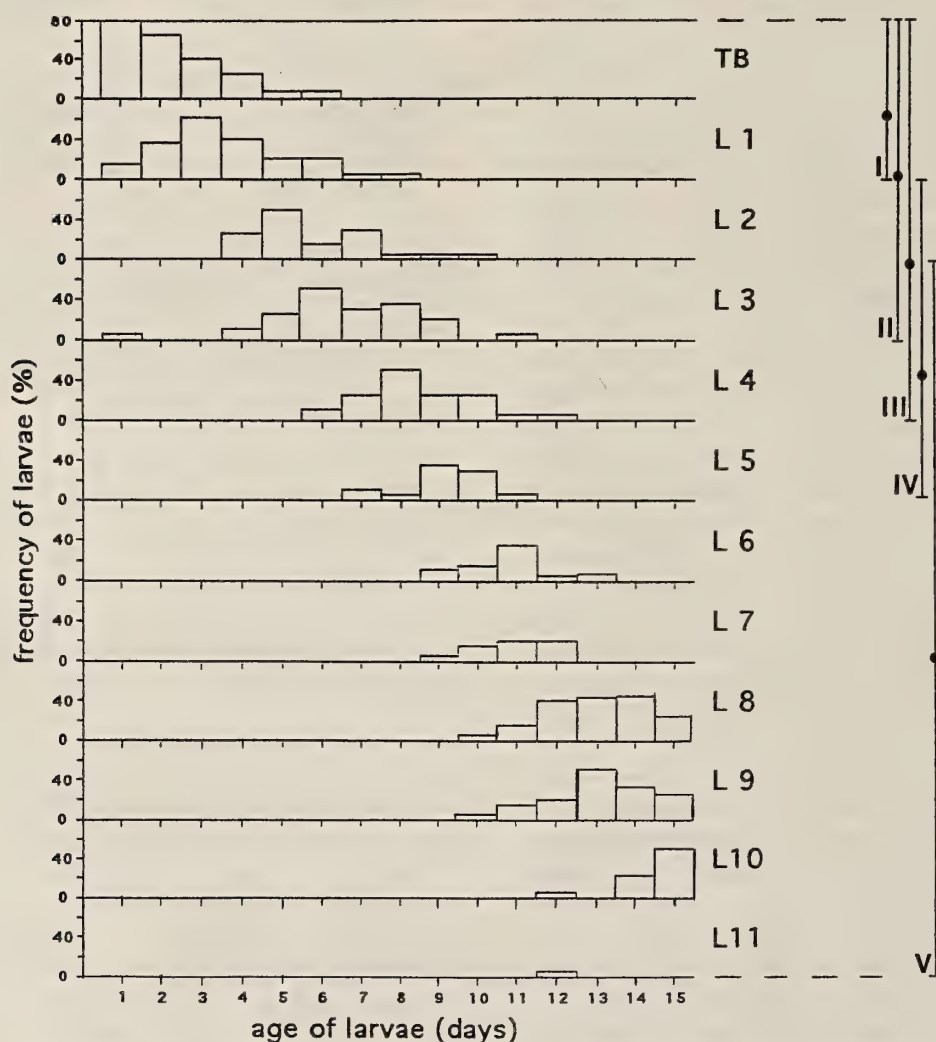


FIG. 2. Sequential feeding pattern of *Heliconius erato* larvae ( $n = 20$ ) in relation to *Passiflora suberosa* leaf age and instar number. TB, terminal bud; L, open leaf. Arabic numbers designate position of leaf in relation to shoot apex. Roman numbers represent larval instars. Closed circles and associated bars denote the median and corresponding interval of leaf age eaten by a given instar.

TABLE 2. Selection by different instars of *Heliconius erato* larvae ( $n = 20$ ) for young vs. old leaves of *Passiflora suberosa*. Data show number of larvae falling into each preference category. See text for description of discrimination categories.

Instar	Preferred leaf category			p*
	Younger	Neutral	Older	
I	20	—	—	< 0.001
II	19	1	—	< 0.001
III	18	1	1	< 0.001
IV	18	1	1	< 0.001
V	9	9	2	< 0.04

\* probabilities calculated from sign tests.

were log transformed for the analysis of variance, following the criteria described in Sokal and Rohlf (1981). Differences among treatments were tested using Fisher's Protected Least Significant Difference multiple comparison tests, when analyses of variance were significant.

To determine specific effects of leaf age on adult size, 40 additional larvae were tested. These were reared on young leaves up to third instar, and after molting for the fourth instar, half of them were kept feeding on young leaves while the remaining fed on mature leaves until pupation. After emergence, adult forewing length was measured, and data were compared through unpaired, two-tailed *t*-tests. There was no indication that size of males and females differed in these experiments, and thus data were grouped. Unless noted measurements are given as mean  $\pm$  standard error.

## RESULTS

In general, the larvae first ate the terminal bud, followed by the first open leaf and progressively devoured older leaves, as they grew (Fig. 2). They consumed all *P. suberosa* shoot parts, including tendrils, stipules and stem. In general, the terminal bud provided enough food to complete the first instar. During this instar some larvae ate part of the first open leaf as well. Leaf damage extended to the third, fourth and fifth open leaves during instars two, three and four, respectively (Fig. 2). There was considerable variation in fifth instar consumption rates. This variation in leaf consumption was expected, because leaves vary in size. About half the larvae required seven open leaves to complete larval development; however, some consumed up to ten leaves before pupation.

Larvae reared on intact *P. suberosa* shoots discriminated between the two leaf categories tested (Table 2). All instars preferred young over mature leaves in the leaf-disk choice test. Type of leaf age offered during fourth instar did not influence choice of larvae during fifth instar (one-tailed sign tests,  $\alpha = 0.05$ ); they

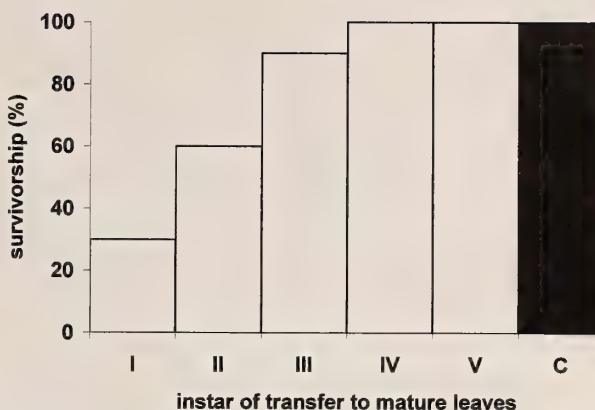


FIG. 3. *Heliconius erato* larval stage survivorship when transferred from young to mature leaves of *Passiflora suberosa* shoots. C, control = treatment 5.

preferred young over mature leaves when reared either on young ( $p < 0.002$ ) or mature ( $p < 0.005$ ) leaves of *P. suberosa*.

Leaf age affected *H. erato* survivorship during early instars (Fig. 3). There was a significant association between the age of transfer to mature leaves and percent survivorship (Spearman's rank correlation test,  $Rho = 0.975$ ,  $n = 5$ ,  $p < 0.05$ ). When transferred to mature leaves during first and second instars only 30% and 60% of larvae respectively survived until pupation (Fig. 3). When transferred to mature leaves during third, fourth and fifth instars, larvae had similar survivorship to those kept on intact shoots (Fig. 3). Larval development rates were significantly longer when larvae were transferred to shoots containing only mature leaves as first or second instars, but there was no effect on later instars (Fig. 4).

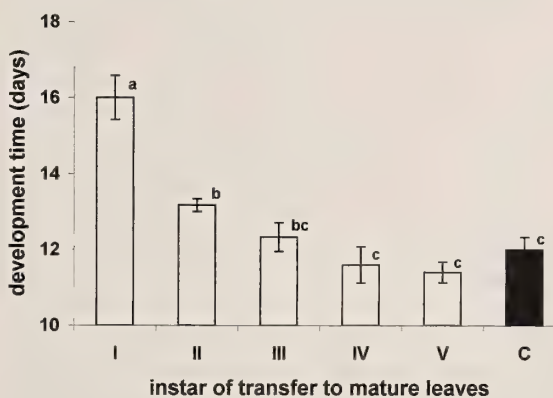


FIG. 4. *Heliconius erato* larval stage development time when transferred from young to mature leaves of *Passiflora suberosa* shoots. C control = treatment 5. Values followed by the same letter are not significantly different (Anova - log transformed data,  $n = 48$ ,  $p < 0.001$ ; Fisher's Protected Least Significant Difference multiple comparison tests,  $p < 0.001$ ).



The size of adults that emerged from larvae transferred during fourth instar to cuttings containing mature leaves ( $36.97 \pm 0.42$  mm) was not significantly different from that of those kept feeding on young leaves ( $38.08 \pm 0.37$  mm) (unpaired, two-tailed *t*-test,  $n = 36$ ,  $p > 0.06$ ). Similarly, the size attained in the adult stage was not affected by transference imposed on all instars in the experiment designed to test effects of leaf age on larval performance (one-way Anova,  $n = 35$ ,  $p > 0.37$ ).

#### DISCUSSION

Our data confirmed field observations in that *H. erato phyllis* larvae feed continuously from the terminal bud (young tissues) to the basal portion (mature leaves) of *P. suberosa* shoots. Young tissues are preferred by all instars, and this preference is related to larval survivorship and development rates. As already pointed out, young larvae move to the terminal bud when placed on any mature leaf. Thus, larvae start feeding on the apical portion of the plant not simply because that is where the female lay the eggs. Larvae begin feeding on the apical portion of *P. suberosa* shoots because the corresponding tissues are more suitable for development of first larval instars. Larvae feed on a wider range of leaf ages in the later instars. A progressive loss in selectivity as larvae age has been found in some insects, however the underlying mechanisms for such an ontogenetic changes still not being clearly understood (Lewis & van Emden 1986). This ontogenetic change in feeding preference may be related to changes in nutrition, plant chemistry or mechanical barriers offered by young and mature *P. suberosa* leaves. Later instars may be better able to overcome defenses of older leaves and differences in food quality have most effect on the early instars; thus, the necessity to make the correct choices may be greatest for early instars (Reavey 1993).

The choice tests showed that later instar larvae prefer young leaves independent of the experience in the previous instar. Thus, they are expected to be found mostly on the youngest surviving portions of host-plants under field conditions. Results also indicated that the age of leaves consumed in a given instar does not influence choices made by larvae during subsequent instar. Even fifth instar larvae, which were comparatively less selective in relation to leaf age, showed preference for young leaves when fed mature leaves during fourth instar. Thus, *H. erato phyllis* larval preference could not be induced in relation to *P. suberosa* leaf age.

Induction of feeding preference, as a result of previous experience regarding particular plant species offered as larval food, has been demonstrated through choice tests performed with several lepidopterans

(Hanson 1983, Bernays & Chapman 1994; but see Bernays & Weiss 1996). Contrary to most of these lepidopterans that are polyphagous, *H. erato* is oligophagous, using a few *Passiflora* species as larval hosts in southern Brazil (Perico & Araújo 1991, Perico 1995). In an additional study carried out in our laboratory, Kerpel (1999) failed to show induction of larval feeding preference regarding the two preferred hosts (*Passiflora misera* and *P. suberosa*) of *H. erato phyllis* in Rio Grande do Sul State.

The data showed that *P. suberosa* leaf age strongly affects *H. erato phyllis* larval performance. Although it is not known to what degree mechanical and nutritional factors contribute to these effects, they may constitute the proximate cause for the maintenance of at least two egg-laying behaviors of *H. erato*. First, it may explain why females selectively oviposit on terminal portion of intact *P. suberosa* shoots (Lopes 1991, Mugrabi-Oliveira & Moreira 1996a); females that eventually oviposit on shoots lacking or with damaged terminal portion may be in disadvantage compared to those laying on intact shoots due to lower larval survivorship and perhaps inferior performance. Second, it may elucidate why females lay only isolated eggs on *P. suberosa* shoots (Mugrabi-Oliveira & Moreira 1996b). By avoiding multiple oviposition they may reduce intraspecific competition for the limited amount of leaves available on many host plants. *H. erato* larvae are cannibalistic, which is also an adaptation to host-plant size limitation (Brower 1997). Mugrabi-Oliveira and Moreira (1996a) found for a *P. suberosa* population of Viamão County, RS, that in more than half of *H. erato* eggs are laid on plants whose total leaf area is less than that required for larval development. Food shortage in the fifth larval instar has profound effects on survivorship and size attained in the adult stage (D. Rodrigues & G. R. P. Moreira unpubl. data).

Thus, we confirm the importance of variation in intraspecific attributes of *P. suberosa* plants, more precisely leaf age, in relation to preference and performance of *H. erato phyllis* larvae. Feeding preferences for young *Passiflora auriculata* tissues had already been demonstrated through choice experiments by Denno and Donnelly (1981) for larvae of *Heliconius sara* in Costa Rica. The physiological basis for such a feeding specialization in earlier instars remains undetermined. It is known that several chemical and physical traits of leaf tissues, such as pubescence, hardness, water content, nutrients and secondary metabolic compounds, vary according to age. It is also known that these leaf characteristics can play a major role in host-plant selection or performance of herbivorous insects (e.g., Scriber 1984, Slansky 1993, Bernays & Chapman 1994, Fernandes 1994), including flea bee-



tles that use *Passiflora* as host plants (Thomas 1987). Smiley and Wisdom (1985) found a significant correlation between leaf nitrogen content of several sympatric *Passiflora* species and larval growth rates of *Heliconius ismenius* and *Heliconius melpomene* in Costa Rica. They, however, failed to find any deleterious effects of potential toxins (including alkaloids, tannins and cyanogenic compounds) on larval growth rates and survivorship. Although not quantified precisely yet, there is a substantial increase in tissue toughness with advance in age in *P. suberosa* leaves. In consequence, ontogenetic changes in leaf age selection could also be associated with morphological constraints on *H. erato phyllis* feeding apparatus. Early instars of some grasshoppers and lepidopterans do not feed upon favored tissue or mature leaves because the mandibles are either not hard enough for effectively chewing, or their gape is not wide enough to grasp thick tissues (Bernays 1991).

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## FIVE NEW SPECIES OF ARGYROTAENIA (TORTRICIDAE: ARCHIPINI) FROM MEXICO AND THE SOUTHWESTERN UNITED STATES

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**ABSTRACT.** Based on an examination of 187 specimens, five new species of *Argyrotaenia* are recognized from Mexico and the southwestern United States. A hypothesis of the phylogenetic relationships among the species is derived using Hennig86 to find the most parsimonious solution to the distribution of 14 morphological characters (5 characters of the forewing, 7 of the male genitalia, and 2 of the female genitalia). *Argyrotaenia spinacallis* Brown & Cramer, new species, from the State of Veracruz, *A. unda* Brown & Cramer, new species, from the states of Mexico and Morelos, and *A. octavana* Brown & Cramer, from the states of Puebla and Veracruz, appear to form a monophyletic group with *A. ponera* (Walsingham), from Puebla. The last is redescribed and illustrated. Although superficially similar, *A. coconinana* Brown & Cramer, new species, from Arizona and New Mexico, and *A. bialbistriata* Brown & Cramer, from Arizona (Cochise Co.) and Durango, Mexico, may not be members of the "*ponera* group" owing to their considerable divergence in male and female genitalia.

**Additional key words:** phylogeny, *ponera* group, morphology, genitalia.

With the exception of a single widespread Palearctic species, the tortricid genus *Argyrotaenia* Stephens is restricted to the New World (Razowski 1997), with about 64 described species occupying portions of the Western Hemisphere from Canada to Argentina. Field work over the past four decades has revealed a surprisingly large number of undescribed species in Central and South America. The purpose of this paper is to describe three of them from central Mexico that appear to form a monophyletic group with *Argyrotaenia ponera* (Walsingham), and two from the southwestern United States and northern Mexico that are superficially similar to *A. ponera*. Although the "*ponera* group" may be confined to Mexico, it is clearly temperate/boreal rather than tropical in origin, restricted to the higher elevations of the Mexican states of Mexico, Morelos, Puebla, and Veracruz. The five new species described herein underscore the considerable alpha-level taxonomic work that remains to be done in the New World south of the United States border.

### MATERIALS AND METHODS

**Material examined.** We examined 187 pinned specimens of adult moths obtained from or studied at the following institutions: American Museum of Natural History (AMNH), New York, New York; The Natural History Museum (BMNH), London, United Kingdom; Canadian National Collection (CNC), Ottawa, Ontario, Canada; Ray B. Nagle private collection (RNC), Tucson, Arizona; Essig Museum of Entomology (UCB), University of California, Berkeley; and National Museum of Natural History (USNM), Smith-

sonian Institution, Washington, DC. Specimens were sorted by geographic location and examined for differences in the male and female genitalia. Genitalia preparations of representative individuals were made following the methodology summarized in Brown and Powell (1991). Male genitalia were photographed using a SONY DKC5000 digital camera and enhanced using Adobe Photoshop. Illustrations of female genitalia were drawn with the aid of a microprojector. Unless indicated otherwise, genitalia illustrations are of a single preparation. Forewing measurements were made with a transparent millimeter ruler under low power of a Leica MZ12 dissecting microscope. Forewing length was measured in a straight line from the base of the wing to the apical region, including the fringe. Forewing width was measured at the widest place on the wing perpendicular to the line measuring length. Where available, 10 individuals of each sex were measured. Photographs were taken with a Wild M 400 microscope with camera attachment. Terminology for wing venation and genitalic structures follows Horak (1984). Abbreviations are as follows: FW = forewing; HW = hindwing; DC = discal cell; ca. = circa (approximately); n = number of individuals or preparations examined;  $\bar{x}$  = mean; Mtns = Mountains; N, S, E, W = compass points.

**Phylogeny.** A phylogenetic analysis was conducted on the 6 species of *Argyrotaenia* suspected to comprise the "*ponera* group" (plus an out-group). The analysis was based on 14 morphological characters (8 binary and 6 multi-state), including 5 characters of the forewing, 7 of the male genitalia, and 2 of the female

TABLE 1. Morphologic characters for cladistic analysis (0 = plesiomorphic state; 1–3 = apomorphic states).

1. FW L:W ratio	0 - 2.3–2.7 1 - 2.8–3.0
2. FW length	0 - 9.0–10.5 mm 1 - 11.0–13.0 mm.
3. FW pattern elements	0 - Without white spot at end of DC 1 - With diffuse white spot at end of DC
4. FW pattern elements	0 - Without pale longitudinal streak 1 - Pale longitudinal streak weak, extending to ca. end of DC 2 - Pale longitudinal streak well-developed, extending beyond end of DC
5. FW pattern elements	0 - Without dark longitudinal streak below distal two-thirds of DC 1 - With dark longitudinal streak below distal two-thirds of DC
6. Shape of valva	0 - Somewhat rounded-triangular 1 - Subrectangular
7. Base of sacculus	0 - Unmodified 1 - With small rounded lobe 2 - With moderate, partially free, rounded lobe 3 - With large, free, rounded lobe
8. Venter of sacculus	0 - Smooth 1 - Slightly bumpy/warty 2 - With spinelike teeth
9. Uncus	0 - Unmodified, moderately broad 1 - Extremely broad
10. Uncus	0 - Unmodified, uniform in width 1 - Slightly tapered distally
11. Aedeagus	0 - Smooth 1 - With 2–4 spinelike teeth at distal end 2 - With 4–6 spinelike near middle 3 - With irregular rows of spinelike teeth from middle to end
12. Aedeagus	0 - About 4 times as long as wide, weakly curved 1 - Greater than 6 times as long as wide, strongly curved
13. Antrum	0 - Small, poorly defined 1 - Well developed, funnel shaped 2 - Large, cup shaped
14. Signum	0 - Lacking sclerotized projections from region bearing capitulum 1 - With sclerotized projection extending anterad from area bearing capitulum. 2 - With sclerotized projection extending posterad from area bearing capitulum.

genitalia. Character state polarity was determined primarily using the out-group method. Although sister-group relationships are virtually unknown for *Argyrotaenia*, recent work by Landry et al. (1999) has identified a monophyletic species group comprised of *A. franciscana* (Walsingham), *A. citrana* (Fernald), *A. citrana isolatissima* Powell, *A. citrana insularis* Powell, *A. niscana* (Kearfott), and an undescribed species; this group was used as the out-group.

**Descriptions of character states.** The character states used in the analysis are described below. Their putative plesiomorphic and apomorphic states are presented in Table 1, and their distribution among the taxa is presented in Table 2.

**Forewing (Characters 1–5).** Most species of *Argyrotaenia*, including the out-group, have a rather broad forewing with a pattern that typically includes one or more oblique fascia and a small, flattened, triangular patch at the costa about two-thirds the distance from the base to the apex. All of the species in the putative “*ponera* group” have a more narrow forewing that lacks the typical *Argyrotaenia* pattern. A forewing

length-to-width ratio of 2.3–2.7, present in the out-group, was considered the plesiomorphic condition (character state 1.0); a forewing length-to-width ratio of 2.8–3.0 was considered the apomorphic condition (character state 1.1). A comparatively small forewing length (9.0–10.5 mm) was assumed to represent the plesiomorphic condition (character state 2.0), and a larger forewing length (11.0–13.0 mm) the apomorphic state (character state 2.1). A forewing without a white spot at the distal end of discal cell was assumed to represent the primitive condition (character state

TABLE 2. Distribution of character states for cladistic analysis (“?” = missing data).

outgroup	000 000 000 000 00
<i>ponera</i>	111 200 310 021 ??
<i>spinacallis</i>	101 000 210 131 11
<i>unda</i>	101 100 110 111 21
<i>octavana</i>	101 100 110 111 20
<i>coconinana</i>	110 211 121 000 02
<i>bialbistrata</i>	100 211 121 000 01



3.0), and a forewing with a diffuse white spot at the end of the discal cell, characteristic of *A. ponera*, *A. spinacallis*, *A. unda*, and *A. octavana*, the apomorphic state (character state 3.1). The absence of a pale longitudinal streak through the discal cell of the forewing was interpreted as plesiomorphic (character state 4.0); the presence of an ill-defined or narrow, pale longitudinal streak extending from the forewing base to about the end of the discal cell, as is present in *A. unda* and *A. octavana*, was interpreted as derived (character state 4.1); and the presence of a well-developed pale longitudinal streak extending from near the base of the forewing to beyond the end of the discal cell, present in *A. ponera*, *A. coconinana*, and *A. bialbistriata*, was considered the most derived state (character state 4.2). The absence of a dark longitudinal streak below the distal two-thirds of the discal cell of the forewing was considered the plesiomorphic condition (character state 5.0), and the presence of a dark longitudinal streak in this region was considered the apomorphic condition (character state 5.1).

Male genitalia (Characters 6–12). A short, somewhat rounded-triangular valva, present in many species of *Argyrotaenia* including the out-group, was considered plesiomorphic (character state 6.0), and a subrectangular valva apomorphic (character state 6.1). An unmodified base of the sacculus was considered plesiomorphic (character state 7.0); the presence of a small, rounded lobe the first step in the transformation series (character state 7.1); the presence of a well-developed, partially free, rounded lobe the next advancement (character state 7.2); and the presence of a large, free, rounded lobe the final step in the series (character state 7.3). The venter of the sacculus is relatively smooth in most species of *Argyrotaenia* (character state 8.0). A slightly bumpy or warty ventral margin was considered derived (character state 8.1), and the presence of spinelike teeth along the margin, characteristic of *A. coconinana* and *A. bialbistriata*, was considered the most derived state (character state 8.2). A moderately broad uncus (character state 9.0) of uniform width (character state 10.0) is present in most species of *Argyrotaenia*. The extremely broad uncus of *A. coconinana* and *A. bialbistriata* was considered the apomorphic condition (character state 9.1). An uncus that is slightly tapered distally also was considered an apomorphic state (character state 10.1). The moderately slender, slight curved aedeagus lacking external spines, present in *A. coconinana* and *A. bialbistriata*, was considered the plesiomorphic state (character state 11.0). An aedeagus with 2–4 spinelike teeth at the distal end (character state 11.1) was considered the first step in a transformation series leading to 4–6

spinelike teeth near the middle of the aedeagus (character state 11.2) and irregular rows of spinelike teeth from near the middle to the distal tip of the aedeagus (character state 11.3). A comparatively short (about 4 times as long as wide), weakly curved aedeagus, present in *A. coconinana* and *A. bialbistriata*, was considered the plesiomorphic state (character state 12.0), and a relatively long (greater than 6 times as long as wide), slender, strongly curved aedeagus (character state 12.1), present in *A. ponera*, *A. spinacallis*, *A. unda*, and *A. octavana*, was considered the apomorphic state.

Female genitalia (Characters 13–14). A small, poorly defined antrum was considered plesiomorphic (character state 13.0); a well developed, funnel-shaped antrum apomorphic (character state 13.1); and a large, cup-shaped antrum the most derived state in the transformation series (character state 13.2). In most *Argyrotaenia* the signum is typical of other members of the tribe Archipini, with a well developed, elongate, interior spine and an external capitulum (see Horak 1984). Because of the extremely variable configuration and development of internal sclerites extending dorsad and posterad from the area bearing the capitulum, we selected the most simple condition, i.e., sclerites absent, as the plesiomorphic state (character state 14.0). The presence of a sclerotized projection extending anterad of the capitulum (character 14.1) was interpreted as apomorphic, and the presence of an additional sclerotized projection extending posterad (character state 14.2) was considered the most derived state.

## RESULTS

The data set was subjected to parsimony analysis using Hennig86 version 1.5 (Lipscomb 1994), employing the "mhennig\*" command. This algorithm constructs trees, each by a single pass through the data, by adding the taxa in a different sequence each time, and then applies branch-swapping to each of the trees. The analysis generated one most parsimonious tree with a length of 27, a consistency index of 0.81, and a retention index of 0.77. The resulting cladogram (Fig. 1) indicates that *A. unda*, *A. ponera*, *A. spinacallis*, and *A. octavana* form a monophyletic group supported by the following characters: 1) diffuse white spot near end of the discal cell of the forewing (character 3); 2) rounded lobe at the base of the sacculus (character 7); 3) spinelike teeth on the aedeagus (character 11); 4) a long, slender, curved aedeagus (character 12); and 5) antrum well developed (character 13). The basal position of *A. coconinana* plus *A. bialbistriata*, with a comparable set of characters supporting their monophyly, suggests that they may not be members of the "*ponera* group" as currently defined. The cladogram (Fig. 1) is

concordant with the geographic distribution of the species (Fig. 2), i.e., *A. unda*, *A. spinacallis*, *A. octavana*, and *A. ponera* occur in close geographic proximity, while *A. coconinana* and *A. bialbistriata* occur relatively far to the north.

All of the species treated herein are distinguished from other *Argyrotaenia* by the absence of the typical semicircular or triangular subapical patch of dark scales on the forewing characteristic of most species, and the presence of a diffuse white dot near the termination of the discal cell or a pale streak through the discal cell. The forewing is more elongate or narrow than most species in the genus: forewing length: width ranges from 2.8–3.0 ( $\bar{x}$  = 2.9;  $n$  = 10) for the included species in contrast to 2.3–2.8 ( $\bar{x}$  = 2.6;  $n$  = 10) for members of the *franciscana* group. According to Powell (pers. comm.), the latter feature is characteristic of cold temperature microlepidoptera in various families (e.g., Elachistidae (Ethmiinae), Tortricidae). The short, somewhat rounded-triangular valvae and broad uncus of the species treated herein are similar to many other congeners, e.g., *A. franciscana* and *A. amatana* (Dyar), and the large, cup-shaped antrum of *A. unda*, new species, is highly reminiscent of that of *A. dichotoma* (Walsingham), of which no males are known.

The dichotomous key below is based on maculation and size of forewing. However, genitalia are much more reliable than facies for species-level identifications, and dissections are recommended. Although males of each species possess at least one diagnostic feature, shapes of the antrum and the signum in the female exhibit considerably more conspicuous and reliable differences.

#### KEY TO THE SPECIES OF THE *PONERA* GROUP

1. Forewing with at least one white or pale yellow longitudinal streak extending through discal cell . . . . . 2
- 1'. Forewing without pale longitudinal streak in discal cell (Fig. 4) . . . . . *spinacallis*
2. Pale longitudinal streak extending along upper portion of discal cell arising at or near base of forewing . . . . . 4
- 2'. Pale longitudinal streak extending along upper portion of discal cell arising approximately one-fourth distance from base to apex of forewing, bordered below in distal two-thirds by a distinct, narrow, dark brown streak . . . . . 3
3. Female with second white streak along lower edge of discal cell; male forewing ground color usually red brown; Durango, Mexico, southeastern Arizona (Fig. 8) . . . . . *bialbistriata*
- 3'. Female without second white streak along lower edge of discal cell; male forewing ground color usually pale brown; Arizona, New Mexico (Fig. 7) . . . . . *coconinana*
4. Forewing length greater than 11.0 mm (Fig. 3) . . . . . *ponera*
- 4'. Forewing length less than 11.0 mm . . . . . 5
5. Forewing with distinct rust-brown dash along costal edge of discal cell in distal one-third; diffuse whitish spot at end of cell (Fig. 5) . . . . . *unda*
- 5'. Forewing lacking distinct rust-brown dash along costal edge of discal cell; fine white dot at end of cell (Fig. 6) . . . . . *octavana*

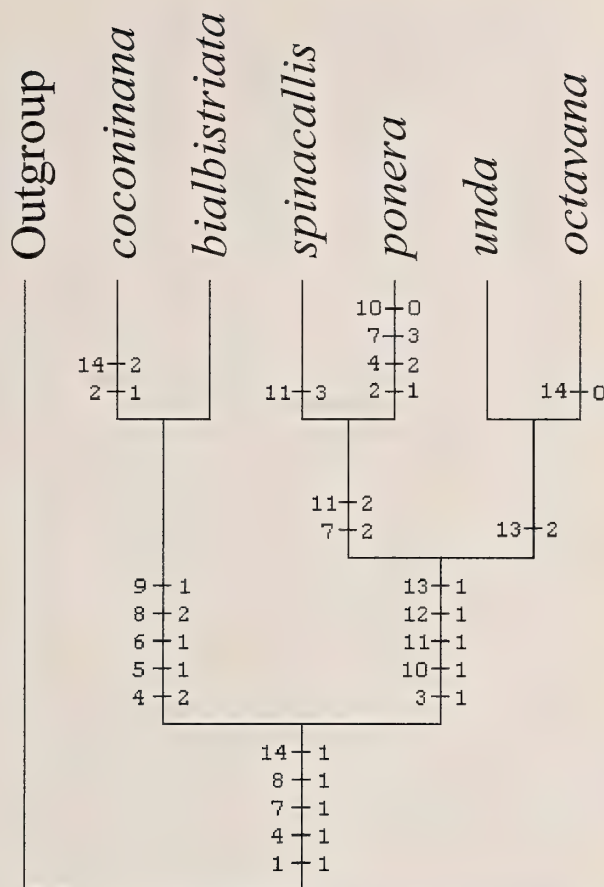


FIG. 1. Hypothesis of phylogenetic relationships among *Argyrotaenia ponera*, *A. spinacallis*, *A. unda*, *A. octavana*, *A. bialbistriata*, and *A. coconinana*. Numbers on the left refer to characters (1–14); numbers on the right refer to character states (e.g., 0 = plesiomorphic, 1–3 = apomorphic) (see Tables 1 and 2).

#### SYSTEMATICS

##### *Argyrotaenia ponera* (Walsingham) (Figs. 3, 9)

*Tortrix ponera* Walsingham, 1914:279.

*Argyrotaenia ponera*: Obraztsov 1961:38; Powell et al. 1995:147.

**Redescription.** Male. Head: Frons with sparse, smooth scaling below mid eye, pale red brown; vertex roughened above, light brownish red. Labial palpus pale red brown mesally, light brownish red laterally. Antennal scaling brown; scape pale red brown, frosted with whitish scales. Thorax: Light brownish copper, lighter mediodorsally. Forewing (Fig. 3): Length 11.0–13.0 mm ( $\bar{x}$  = 12.2;  $n$  = 10). Upper side light brown; a conspicuous silver-white longitudinal streak extending from base, ending in a distinct silver-white dot just beyond end of DC, more diffuse and ill-defined from spot to termen; an ill-defined, darker brownish copper longitudinal streak immediately above white longitudinal streak; a small patch of darker brownish copper scales below silver-white streak beyond end of DC, accentuating silver-white dot near end of DC. Fringe pale gray. Under side pale gray. Hindwing: Upper side pale gray. Fringe slightly lighter than ground color. Under side pale gray. Genitalia: As in Fig. 9 (photograph of JWB slide 1035, Puebla, Mexico; 3 preparations examined). Uncus moderately broad, uniform in width, with truncate tip. Socius short, fused with tegumen. Arms of gnathos narrow,





FIG. 2. Geographic distribution of *Argyrotaenia ponera* (star), *A. spinacallis* (open square), *A. unda* (closed triangles), *A. octavana* (closed squares), *A. bialbistriata* (open circles), and *A. coconinana* (closed circles).

uniform in width, united distally into an elongate pointed tip. Transtilla a simple, sclerotized, narrow band. Valva short, somewhat rounded-triangular, costa undifferentiated; sacculus moderately long, slender, curved, ending ca. 0.8 distance from base to apex; base of sacculus with large, free, semicircular lobe; venter of distal 0.5 of sacculus with small bumps. Aedeagus long, slender, curved, with 4-6 spinelike teeth near the middle along right side; cornuti not evident

(deciduous and lost); phallobase moderate, slightly swollen distad to attachment point of juxta.

**Female.** Unknown.

**Holotype** ♂, Mexico [Puebla], Popocatepetl Park, 13,000' [4000 m], 6047 Wlsm 1908 (Wm. Schaus, USNM).

**Paratypes.** Same data as holotype, 1 ♂, "co-type," 33946 (BMNH), 1 ♂, "co-type," 33947 (BMNH).

**Additional specimens examined.** MEXICO: Puebla: Popocatepetl Park, 13,000' [4000 m], 1 ♂ (USNM), 1 ♂, "co-type" Wslm 6048 (USNM); Tlmacas, Volcan Popocatepetl, 3600–3660 m, 7 ♂, 24 August 1987 (J. Brown & J. Powell, UCB).

**Diagnosis.** *Argyrotaenia ponera* is superficially most similar to *A. coconinana*, from which it can be distinguished by the following features: 1) ground color of the forewing brownish copper rather than pale brown, lacking a distinct dark brown streak below silver-white streak; 2) large, well-defined lobe at the base of the sacculus, less defined in *A. coconinana*; 3) ventral edge of the distal 0.5 of the sacculus bumpy rather than dentate; and 4) aedeagus longer and more evenly curved, with 4–6 spinelike teeth near the middle.

**Remarks.** Walsingham (1914:279) had 4 specimens when he described *Tortrix ponera*: one was designated as the holotype ["HT"] (USNM) and two as paratypes ["PT"] (BMNH), although the latter two are labeled as "co-types." The fourth specimen (6048 Wslm) also is labeled "co-type" but was not designated as a paratype in the original description—it is referred to only after the locality data: "Four specimens." There is one additional specimen (USNM) with identical collecting data that was not mentioned (or seen?) by Walsingham. Obraztsov's (1961:35) illustration of *A. ponera* includes a photograph of an aedeagus, which is not that of the holotype of *A. ponera*.

### *Argyrotaenia spinacallis* Brown & Cramer, new species

(Figs. 4, 11, 15)

**Description.** Male. Head: Frons with sparse, smooth scaling below mid eye, pale red brown; vertex roughened above, pale red brown. Labial palpus pale yellow mesally, pale red brown laterally. Antennal scaling light brown; scape brown, with pale red-brown scales. Thorax: Light brown. Forewing (Fig. 4): Length 9.5–10.5 mm ( $\bar{x}$  = 10.0;  $n$  = 10). Upper side with costal one-half mostly copper brown, lower one-half pale yellow orange; distal one-third faintly reticulated; occasionally with ill-defined, thin, pale red-brown longitudinal streak along lower edge of DC; a pair of diffuse, small, dark-brown spots near distal end of DC, separated by diffuse white streak. Fringe pale red brown with basal row of slightly darker red-brown scales. Under side pale gray. Hindwing: Upper side pale gray. Fringe concolorous with hindwing. Under side pale gray. Genitalia: As in Fig. 11 (photograph of JWB slide 1063, Veracruz, Mexico; 3 preparations examined). Uncus moderately broad, with truncate tip. Socius short, fused to tegumen. Gnathos united distally into moderately long, pointed tip. Transtilla a simple, sclerotized, narrow band. Valva short, somewhat rounded-triangular, costa undifferentiated; sacculus moderately long, curved, attenuate distally, ending in a short free tip ca. 0.85 distance from base to apex; sacculus with moderately large, rounded, partially free lobe at base; venter of sacculus weakly dentate in distal 0.25. Aedeagus moderately long, slender, curved near middle; irregular rows of spinelike teeth from near middle to distal end of aedeagus. Cornuti not evident (deciduous and lost).

**Female.** FW length 9.3–9.5 mm ( $\bar{x}$  = 9.4;  $n$  = 2). Essentially as described for male, except hindwing with pale gray-brown overscaling. Genitalia: As in Fig. 15 (drawn from JWB slide 1036, Veracruz, Mexico; 2 preparations examined). Papillae anales unmodified, broad. Sterigma a slender, strongly sclerotized, weakly undulate band; ostium bursae moderately broad; antrum large, funnel shaped, with long ventral tube, strongly sclerotized. Ductus bursae moderately long, with distinct junction between corpus bursae and ductus bursae. Corpus bursae ovoid; signum with sclerite extending posterad of capitulum greatly reduced, portion extending anterad well developed.

**Holotype** ♂, Mexico, Veracruz, Cañon de las Minas, 13 km NE Perote, 2150 m, 18 August 1987 (J. Brown & J. Powell, UCB).

**Paratypes.** Same data as for holotype, 20 ♂, 2 ♀, 18/19 August 1987 (J. Brown & J. Powell, UCB), 1 ♂, 19 August 1987 (J. Doyen, UCB).

**Additional specimen examined.** MEXICO: Mexico: La Marquesa, 1 ♂, 13 July 1966 (O. Flint & A. Ortiz, USNM).

**Diagnosis.** *Argyrotaenia spinacallis* differs from all other species in the group by the absence of the pale longitudinal streak

on the forewing. Average male forewing length (10.0 mm) is less than that of *A. ponera* (12.2 mm) and *A. coconinana* (12.2 mm) and slightly greater than that of *A. unda* (9.4 mm) and *A. octavana* (9.4 mm). The female genitalia of *A. spinacallis* are distinguished easily from all other species by the strongly sclerotized, funnel-shaped antrum. In comparison with *A. ponera*, the male genitalia have slightly shorter, more rounded valvae; a slightly less well-developed rounded lobe at the base of the sacculus; and a slightly longer aedeagus, with irregular rows of spinelike teeth from near the middle to the distal end. The somber forewing pattern, spinelike teeth of the aedeagus in the male, and funnel-shaped antrum in the female easily separate this species from other members of the *ponera* group.

**Remarks.** The single male from La Marquesa is similar to *A. spinacallis* in general appearance, but has a larger forewing length (10.8 mm) and a darker brown ground color. Because the genitalia slide (Razowski no. 11072) apparently is lost, comparison of these structures is impossible; hence the specimen is not included in the type series. In addition to the locality and slide labels, the specimens bears a label indicating "Holotype" and one indicating "*Argyrotaenia ?ponera* Wslm.," probably referring to *A. ponera*.

**Etymology.** The species name refers to the irregular rows of spinelike teeth on the aedeagus.

### *Argyrotaenia unda* Brown & Cramer, new species

(Figs. 5, 10, 16)

**Description.** Male. Head: Frons with sparse, smooth scaling below mid eye, copper brown; vertex roughened above, yellowish white. Labial palpus pale red brown mesally, light copper laterally. Antennal scaling pale red brown; scape copper orange, with pale red-brown frosting. Thorax: Copper orange. Forewing (Fig. 5): Length 9.0–10.0 mm ( $\bar{x}$  = 9.4;  $n$  = 10). Upper side rust to light copper, rust brown apically; conspicuous thin, silver-white longitudinal streak from base to beyond middle of DC; an ill-defined pale-brown line immediately below silver-white streak; conspicuous rust brown streak along distal one-third of costal edge of DC, bordered above by diffuse white scaling, terminating in a diffuse silver-white spot. Fringe pale red brown. Under side light gold. Hindwing: Upper side white. Fringe yellowish white. Under side yellowish white. Genitalia: As in Fig. 10 (photograph of JAP slide 6271, Mexico, Mexico; 3 preparations examined). Uncus moderately broad, slightly tapered distally, with truncate tip. Socius, gnathos, and transtilla as in *ponera* and *spinacallis*. Valva short, costa slightly arched dorsally, with a lightly sclerotized subrectangular lobe near base; sacculus moderately long, curved, attenuate distally, ending in a short free pointed tip; base of sacculus with an ill-defined, semicircular lobe. Aedeagus moderately long, not as strongly bent as in *ponera* and *spinacallis*; distal end with 2–4 small spinelike teeth; cornuti 12–15 in a dense fascicle.

**Female.** FW length 9.0–10.0 mm ( $\bar{x}$  = 9.4;  $n$  = 6). Essentially as described for male, except hindwing with gray-brown overscaling. Genitalia: As in Fig. 16 (drawn from JAP 6272 slide, Mexico, Mexico; 3 preparations examined). Papillae anales unmodified, broad. Sterigma moderately heavily sclerotized; ostium bursae moderately small, somewhat crescent shaped; antrum extremely large, cup shaped, strongly sclerotized. Ductus bursae moderately long, with distinct junction between corpus bursae and ductus bursae; posterior one-third of ductus bursae broad, strongly sclerotized. Corpus bursae ovoid; signum with sclerite extending posterad of capitulum reduced; anteriorly-directed sclerite extremely elongate, attenuate, extending nearly to anteriormost wall of corpus bursae as narrow line.

**Holotype** ♂, Mexico, Mexico, 7 air km WSW Juchitepec, 2750 m, 24 August 1987 (J. Brown & J. Powell, UCB).

**Paratypes.** MEXICO: Mexico: same data as for holotype, 10 ♂, 3 ♀, 24/25 August 1987 (J. Brown & J. Powell, UCB); 10 air km SE Amecameca, 2720 m, 1 ♂, 23 August 1987 (J. Brown & J. Powell, UCB). Morelos: Lag. Zempoala, 3 ♀, 10/11 July 1965 (O. Flint & A. Ortiz, USNM).

**Diagnosis.** *Argyrotaenia unda* is superficially and genitally most similar to *A. octavana*. In facies most specimens of *A. unda* can





FIGS. 3-8. Adults of *Argyrotaenia*. 3. *A. ponera*; 4. *A. spinacallis*; 5. *A. unda*; 6. *A. octavana*; 7. *A. coconinana*; 8. *A. bialbistriata*.



be distinguished from the latter by a more isolated, narrow, dark rust-brown dash along the costal edge of the discal cell in the distal one-third, although this character is not always obvious. Likewise, male genitalia are not easily separated. In contrast, the female genitalia are separated easily from those of *A. octaviana* by the large, cup-shaped antrum and by the extremely elongate, slender, anteriorly-directed sclerite from the base of the area that bears the capitulum.

**Comments.** The female genitalia of *A. unda* are similar to those of *A. dichotoma* (Walsingham) (illustrated in Obratzov 1961:30) in the presence of a large, cup-shaped antrum. However, the adult of *A. dichotoma*, a large, dark-brown moth, with an ill-defined grayish spot near the end of the discal cell and a white hindwing, is superficially quite dissimilar to *A. unda*. It is possible that *A. dichotoma* is a member of the *ponera* group, based on the similarity of the female genitalia to those of *A. unda* and the pale spot at the end of the discal cell, but in the absence of a male (i.e., the species is known only from two females from Guatemala), its assignment to the group would be speculative. While its forewing is narrow like other members of the *ponera* group (i.e., L:W = 2.88), the slightly undulate costa is not consistent with members of this group. It is unusual that Obratzov (1961) figured the female genitalia of *A. dichotoma* but did not discuss it or formally propose a new combination in the text.

**Etymology.** The species name is Latin for "wave."

### *Argyrotaenia octaviana* Brown & Cramer, new species

(Figs. 6, 12, 17)

**Description.** Male. Head: Frons with sparse, smooth scaling below mid eye, copper brown; vertex roughened above, yellowish white. Labial palpus pale red brown mesally, light copper laterally. Antennal scaling pale red brown; scape copper orange, with pale red-brown frosting. Thorax: Copper orange. Forewing (Fig. 6): Length 9.0–10.0 mm ( $\bar{x}$  = 9.4;  $n$  = 10). Upper side rust to light copper, pale rust brown apically; narrow, pale yellow-brown streak through lower half of discal cell; fine silver-white dot at end of discal cell; thin, silver-white longitudinal line from base to beyond middle of DC. Fringe pale red brown. Under side light gold. Hindwing: Upper side white. Fringe yellowish white. Under side yellowish white. Genitalia: As in Fig. 12 (photograph of JWB slide 1057, Mexico, Mexico; 5 preparations examined). Uncus moderately broad, slightly tapered distally, with truncate tip. Socius, gnathos, and transtilla as in *unda*. Valva short, costa slightly arched dorsally, with a lightly sclerotized subrectangular lobe near base; sacculus moderately long, curved, attenuate distally, ending in a short free pointed tip; base of sacculus with an ill-defined, semicircular lobe. Aedeagus moderately long, not as strongly bent as in *ponera* and *spinacallis*; distal end with 2–4 small spine-like teeth; cornuti 12–15 in a dense fascicle.

**Female.** FW length 8.0 mm ( $n$  = 1). Essentially as described for male, except smaller forewing length and hindwing with dense gray-brown overscaling. Genitalia: As in Fig. 17 (drawn from JWB 1137 slide, Mexico, Veracruz; 1 preparation examined). Papillae anales unmodified, broad. Sterigma moderately heavily sclerotized; ostium bursae moderate in size; antrum a deep, slightly tapered, strongly sclerotized cup. Ductus bursae moderately long, with distinct junction between corpus bursae and ductus bursae. Corpus bursae ovoid; signum an irregular sclerotized patch bearing the capitulum and long spine; posterior- and anterior-directed sclerites absent.

**Holotype** ♂, Mexico, Puebla, 10 km E Esperanza, 15 August 1987 (J. Brown & J. Powell, UCB).

**Paratypes.** MEXICO: Puebla: 10 km E Esperanza, 27 ♂, 15 August 1987 (J. Brown & J. Powell, UCB); 10 rd km E Escalante [probably a *lapsus* of Esperanza], 4 ♂, 15 August 1987 (J. Brown & J. Powell, UCB). Veracruz: 22 rd km W Ciudad Mendoza, 2150 m, 12 ♂, 1 ♀, 13 August 1987 (J. Brown & J. Powell, UCB).

**Diagnosis.** *Argyrotaenia octaviana* is most similar to *A. unda*, from which it can be distinguished by the characters described in the diagnosis of *A. unda* above.

**Etymology.** The species name refers to the eighth month of the year—all specimens were collected in August.

### *Argyrotaenia coconinana* Brown & Cramer, new species

(Figs. 7, 14, 19)

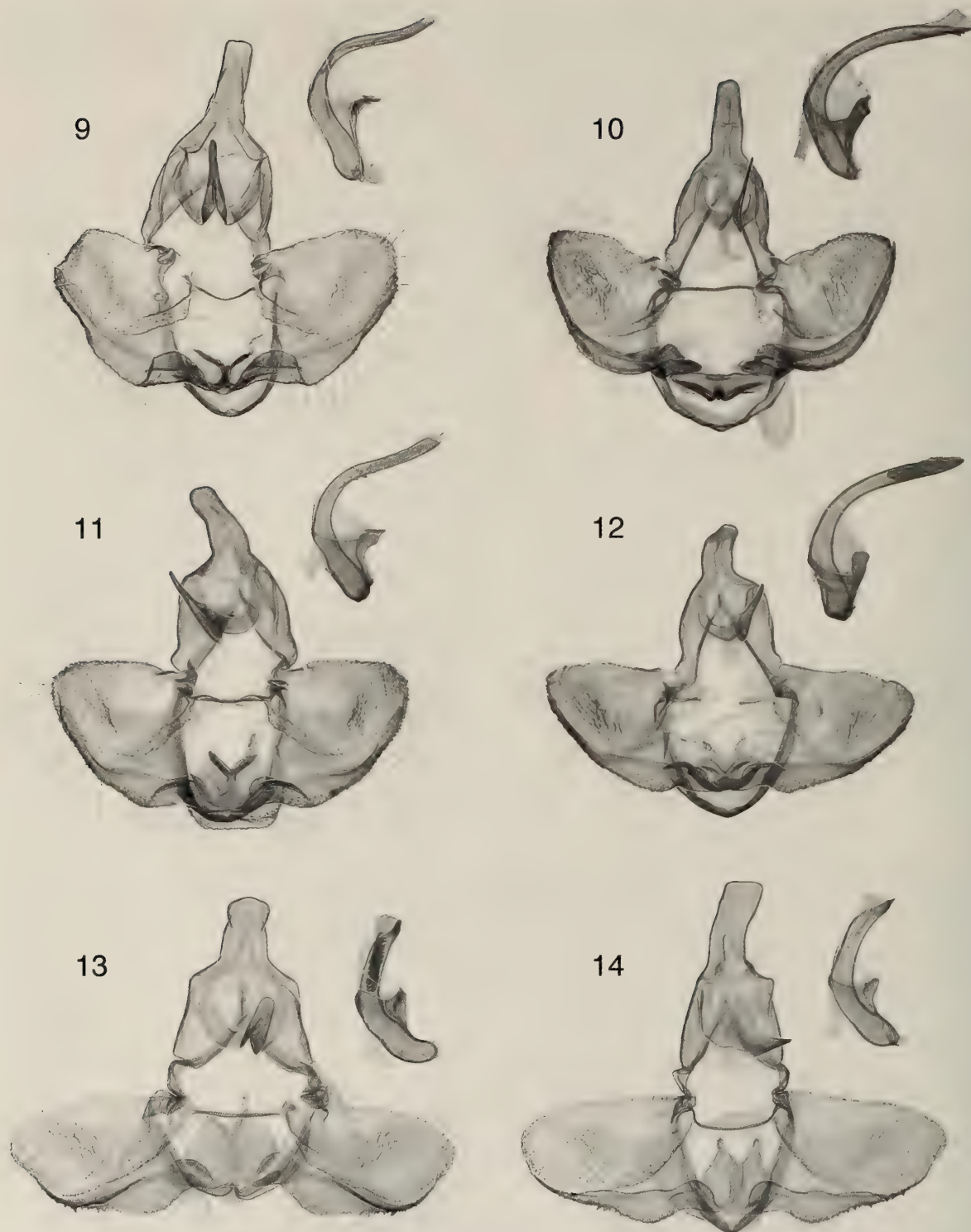
**Description.** Male. Head: Frons with sparse, smooth scaling below mid eye, pale red brown; vertex roughened above, pale red brown. Labial palpus light pale red brown mesally, slightly darker pale red brown laterally. Antennal scaling brown; scape pale red brown, with yellowish white scales. Thorax: Pale brown gold. Forewing (Fig. 7): Length 11.0–13.0 mm ( $\bar{x}$  = 12.2;  $n$  = 10). Upper side pale red brown; a whitish to yellowish-white longitudinal streak extending from near base toward termen through DC; a faint, ill-defined, pale red-brown line immediately above yellowish-white streak, and a well-defined dark copper-brown line immediately below; a well-defined, short line in apical region concolorous with line below yellowish-white streak. Fringe mostly yellowish white, with some pale red brown distally. Under side pale gray. Hindwing: Upper side white, with pale gray overscaling. Fringe concolorous with hindwing. Under side pale gray. Genitalia: As in Fig. 14 (drawn from USNM slide 89386, Arizona, USA; 4 preparations examined). Uncus extremely broad, uniform in width or slightly expanded distally, with truncate tip. Socius small, fused to tegumen. Arms of gnathos moderately long, united distally into pointed tip. Transtilla a simple, sclerotized, narrow band. Valva long, subrectangular, costa weakly arched downward at apex; sacculus moderately long, curved, extending ca. 0.8 distance from base to apex, attenuate distally, conspicuously dentate in distal 0.25. Aedeagus comparatively short, evenly curved near middle; weakly notched distally, with mesal, sclerotized, thornlike process and weak, short, subdistal, accessory lobe; vesica with fascicle of 10–15 long, slender cornuti, curved at base and in distal 0.1.

**Female.** FW length 11.0–12.0 mm ( $\bar{x}$  = 11.4;  $n$  = 10). Essentially as described for male, except slightly greater forewing length. Genitalia: As in Fig. 19 (drawn from USNM slide 89387, Arizona, USA; 5 preparations examined). Papillae anales moderately large, flat. Sterigma a slender, strongly sclerotized, rounded band, with a lightly sclerotized disc mesally; ostium bursae slightly recessed; antrum small, in the form of a short, sclerotized, incomplete band at junction of ostium bursae and ductus bursae (=colliculum?). Ductus bursae moderately long, with distinct junction between corpus bursae and ductus bursae. Corpus bursae ovoid; signum with large, subtriangular, sclerotized flanges projecting anterad and posterad from capitulum.

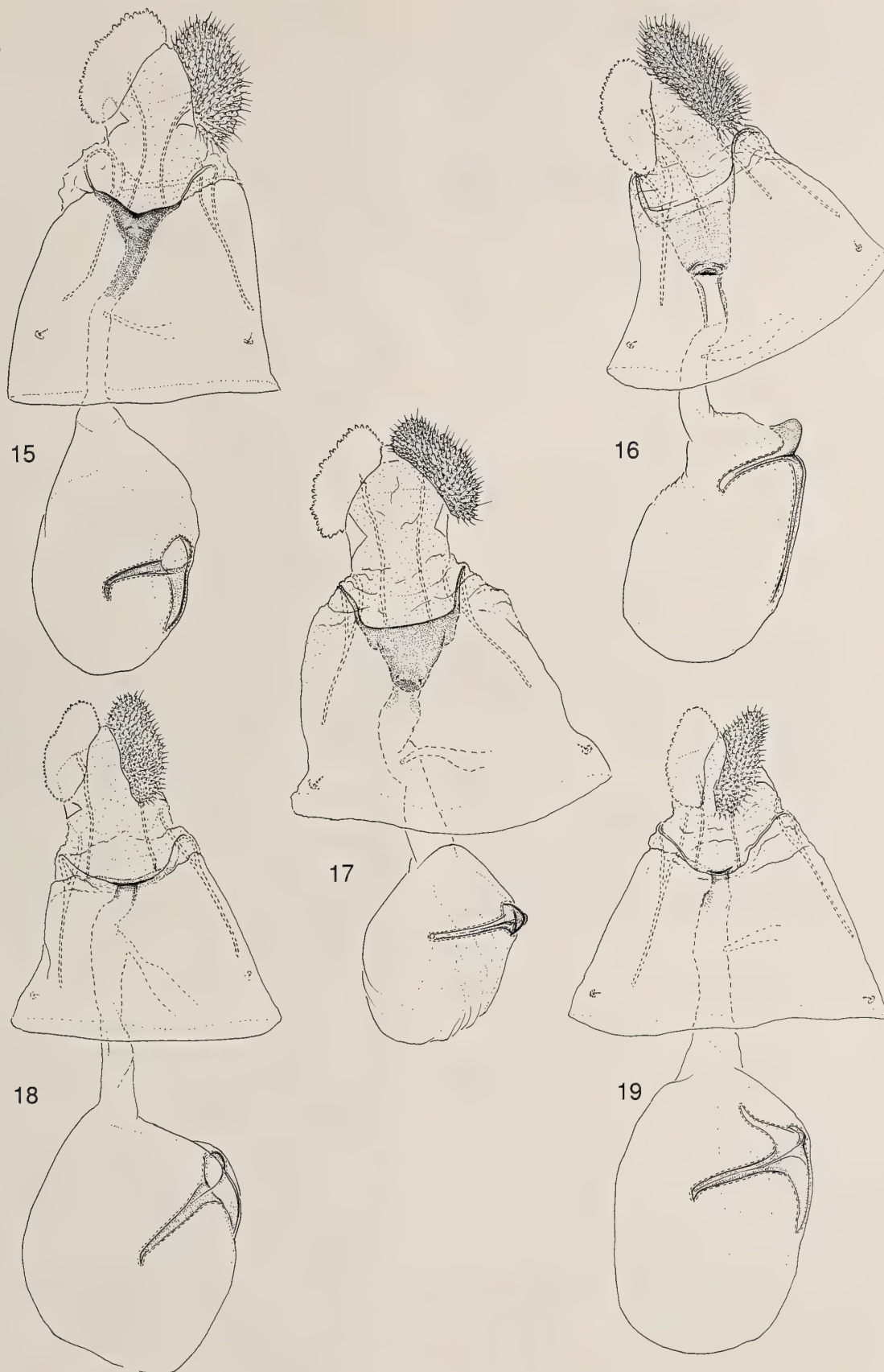
**Holotype** ♂, USA, Arizona, Coconino Co., Hochderffer Hill, 12.5 mi [20 km] NNW Flagstaff, 8500' [2615 m], 16 July 1964 (J. G. Franclemont, USNM).

**Paratypes.** USA: ARIZONA: Coconino Co.: Same locality as for holotype, 14 ♂, 16 July 1964, 4 ♂, 1 ♀, 17 July 1964, 1 ♂, 18 July 1964, 1 ♂, 2 ♀, 19 July 1964 (all J. G. Franclemont, USNM, UCB, BMNH); Fort Valley, 7.5 mi [12 km] NW Flagstaff, 7350–7500' [2262–2308 m], 1 ♂, 26 June 1961, 1 ♂, 6 July 1961, 4 ♂, 9 July 1961, 1 ♀, 11 July 1961, 2 ♂, 12 July 1961 (all R. W. Hodges, USNM), 1 ♂, 4 July 1964, 5 ♂, 8 July 1964, 2 ♂, 11 July 1964, 5 ♂, 13 July 1964, 6 ♂, 14 July 1964, 1 ♂, 15 July 1964, 5 ♂, 16 July 1964, 1 ♂, 17 July 1964 (all J. G. Franclemont, USNM); West Fork, 16 mi [25.5 km] SW Flagstaff, 6500' [2000 m], 2 ♂, 4 July 1961, 1 ♂, 8 July 1961, 2 ♂, 1 ♀, 13 July 1961, 1 ♀, 19 July 1961 (all R. W. Hodges, USNM), 2 ♂, 3 July 1964 (J. G. Franclemont, USNM); West Fork Oak Creek, 19 road mi [30.4 km] SW Flagstaff, 6500' [2000 m], 1 ♂, 13 July 1995, 2 ♂, 16 July 1995 (J. Powell & F. Sperling, UCB); Walnut Canyon, 6.3 mi [10 km] ESE Flagstaff, 6500' [2000 m], 5 ♂, 5 July 1965 (J. G. Franclemont, USNM), 1 ♂, 14 July 1995, bl. (J. Powell & F. Sperling, UCB). Cochise Co.: Rustler Park, Chiricahua Mts., 8500' [2615 m], 1 ♀, 3 July 1972, 1 ♂, 12 July 1972, 1 ♀, 14 July 1972, 1 ♀, 27 July 1972, at light (J. Powell, UCB); East Turkey Creek, Chiricahua Mts., 6400' [1970 m], 1 ♀, 16 June 1966 (J. G. Franclemont, USNM).





FIGS. 9-14. Male genitalia of *Argyrotaenia*. 9. *A. ponera*; 10. *A. unda*; 11. *A. spinacallis*; 12. *A. octavana*; 13. *A. bialbistrana*; 14. *A. coconinana*.



FIGS. 15–19. Female genitalia of *Argyrotaenia*. 15. *A. spinacallis*; 16. *A. unda*; 17. *A. octavana*; 18. *A. bialbistriata*; 19. *A. coconinana*.



Pima Co.: Summerhaven, Mount Lemon, 1 ♀, 21 July 1995, 1 ♀, 9 July 1996 (R. Nagle, RNC). NEW MEXICO: Grant Co.: Cherry Creek Camp, 13 mi [20.8 km] N Silver City, 6900' [2123 m], 1 ♂, 1 ♀, 10 July 1964 (F. E. & M. Rindge, AMNH).

**Diagnosis.** *Argyrotaenia coconinana* is most similar to *A. bialbistriata*, and their specific distinctness is not entirely certain. The two can be separated by the following: (1) in females of *A. bialbistriata* the longitudinal streak through the discal cell is always silver-white rather than yellowish white or pale cream, and there is a second silver-white longitudinal streak along the lower edge of the discal cell; (2) males of *A. bialbistriata* have considerably darker scaling bordering the lower edge of the pale forewing longitudinal streak and in the apical region; (3) males and females of *A. coconinana* have a greater forewing length; and (4) the signum of *A. coconinana* has a well developed, triangular sclerite projecting posterad from the capitulum that is lacking in *A. bialbistriata*.

**Etymology.** The species name is derived from the county of Coconino in Arizona.

### *Argyrotaenia bialbistriata* Brown & Cramer, new species

(Figs. 8, 13, 18)

**Description.** Male. Head: Frons with sparse, smooth scaling below mid eye, pale red brown; vertex roughened above, pale red brown. Labial palpus pale red brown mesally, slightly darker red brown laterally. Antennal scaling brown; scape pale red brown, with yellowish white scales. Thorax: Pale brown-gold. Forewing (Fig. 8): Length 9.8–9.9 mm ( $\bar{x}$  = 9.8;  $n$  = 2). Upper side pale red brown; a whitish to yellowish-white longitudinal streak extending from near base toward termen through DC; a faint, ill-defined, pale red-brown line immediately above yellowish-white streak, and a well-defined dark copper-brown line immediately below; a well-defined, short line in apical region concolorous with line below yellowish-white streak. Fringe mostly yellowish white, with some pale red brown distally. Under side pale gray. Hindwing: Upper side white, with pale gray overscaling. Fringe concolorous with hindwing. Under side pale gray. Genitalia: As in Fig. 13 (photograph of JWB slide 1091; Durango, Mexico; 2 preparations examined). Uncus extremely broad, uniform in width, with truncate tip. Socius small, fused to tegumen. Arms of gnathos moderately long, united distally into pointed tip. Transtilla a simple, sclerotized, narrow band. Valva long, subrectangular, costa weakly arched downward at apex; sacculus moderately long, curved, extending ca. 0.8 distance from base to apex, attenuate distally, conspicuously dentate in distal 0.25. Aedeagus comparatively short, curved near middle; weakly notched distally, with mesal, sclerotized, thornlike process and weak, short, subdistal, accessory lobe; vesica with fascicle of 10–15 long, slender cornuti, curved at base and in distal 0.1.

**Female.** FW length 9.5–10.0 mm ( $\bar{x}$  = 9.7;  $n$  = 3). Essentially as described for male, except forewing maculation much more pale, with a second whitish longitudinal streak along the lower edge of the discal cell. Genitalia: As in Fig. 18 (drawn from JWB slide 1110, Durango, Mexico; 3 preparations examined). Papillae anales moderately large, flat. Sterigma a slender, strongly sclerotized, rounded band, with a lightly sclerotized disc mesally; ostium bursae slightly recessed; antrum small, in the form of a short, sclerotized, incomplete band at junction of ostium bursae and ductus bursae (=colliculum?). Ductus bursae moderately long, with distinct junction between corpus bursae and ductus bursae. Corpus bursae ovoid; signum without sclerotized projection posterad of capitulum.

**Holotype** ♂, Mexico, Durango, 10 mi (16 km) W El Salto, 9000' [2769 m], 6 June 1964 (J. E. H. Martin, CNC).

**Paratypes.** MEXICO: Durango: 10 mi (16 km) W El Salto, 9000' [2769 m], 1 ♂, 1 ♀, 6 June 1964 (J. E. H. Martin, CNC).

**Additional specimens examined.** USA: Arizona: Cochise Co.: Barfoot Park, Chiricahua Mts., 8500' [2615 m], 1 ♀, 14 June 1985 (P. Jump, UCB); Rustler Park, Chiricahua Mtns, 8500' [2615 m], 1 ♀, 3 July 1972, at light (J. Powell, UCB).

**Diagnosis.** As mentioned in the diagnosis of *A. coconinana*, *A. bialbistriata* is extremely similar to the latter. The most conspicuous character separating the two is the shape of the signum in the female. In *A. bialbistriata* the signum always lacks the large, distally attenuate projection posterad of the capitulum that is always well developed in *A. coconinana*.

**Comments.** The two female specimens cited above from the Chiricahua Mountains of southeastern Arizona present somewhat of an enigma, suggesting the sympatric and synchronic occurrence of *A. bialbistriata* and *A. coconinana* in the Chiricahua Mountains. There are at least two different interpretations of this information. (1) The two species are sympatric and synchronic in the Chiricahua Mountains of southeastern Arizona, and can be separated by differences in the shape of the signum. This interpretation is supported further by a number of qualitative characters listed in the diagnosis of *A. coconinana*. (2) The two are conspecific, and the apparently distinct shape of the signum and other qualitative differences merely represent infraspecific variation. Although this explanation may be correct, there are no intermediate expressions of the signum shape; i.e., all females throughout the range of *A. coconinana* (except for the two females from the Chiricahua Mountains) are extremely consistent in this character state.

The apparent disjunct occurrence of *A. bialbistriata* in the Chiricahua Mountains of southeastern Arizona and Durango, Mexico, is illustrated by several other Lepidoptera, e.g., *Sparganopseustis martinana* Powell (Tortricidae) (Powell 1986), *Dorithia trigonana* Brown & Obraztsov (Tortricidae) (Brown & Powell 1991), and *Hypaurotis crysalus* (Edwards) (Lycaenidae) (Brown 1989).

**Etymology.** The species name refers to the two white longitudinal streaks of the forewing of the female.

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# GENERAL NOTES

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## FIELD OBSERVATIONS ON LARVAL DIAPAUSE IN THE FLORIDA VICEROY, *LMENITIS ARCHIPPUS FLORIDENSIS*

**Additional key words:** hibernacula, photoperiod, subspecies, thermoperiod.

Recent publications treating nymphaline butterflies of Florida do not mention the occurrence of diapause in the Florida viceroy, *Limenitis archippus floridensis* (Stkr.) (Gerberg & Arnett 1989, Minno & Emmel 1993, Smith et al. 1994, Emmel 1997). In addition, Williams and Platt (1987) could not induce diapause in laboratory strains of *L. a. floridensis* derived from wild stock from Dade Co. No diapause occurred among 220 larvae in three broods reared under laboratory controlled conditions ( $25 \pm 2^\circ\text{C}$ ) with photoperiods ranging from 8L:16D to 18L:6D, and they speculated (p. 351) that "... a high proportion of the Florida subspecies may have lost the ability to construct hibernacula and enter diapause in the third instar." Here we report that some individuals in natural populations of *L. a. floridensis* do, in fact, begin to diapause in northcentral and southwestern Florida, whereas, others apparently remain "on the wing" throughout the year.

Three separate field observations of apparent diapause were made by us during 1995 and 1996 (Table 1). Each involved the collecting of either hibernacula and (or) larvae from foliage of willow, *Salix caroliniana* L. (Salicaceae). All of the hibernacula were found between 1.5–2.5 m above the substrate. The five occupied hibernacula each contained a third instar larva (in apparent diapause). Only one of the hibernacula we found had had its larva eaten by a small insectivorous bird, as evidenced by a small hole having been pecked into the basal portion of the empty hibernaculum. Since there was evidence of larval feeding on the branches supporting these hibernacula, we suspect that the remaining larvae had completed development and had left their foodplants to pupate.

At the Everglades locality, one egg, one second instar larva on its perch, and two fifth instar larvae also were observed alongside the three occupied hibernacula during late January. Adult *L. a. floridensis* also were seen on the wing at the Corkscrew Park and Everglades Localities. At the Gainesville locality, the 25 unoccupied hibernacula apparently had recently been vacated by larvae, since their silken girdles covered the newly emerging spring buds, and their color was a copper-brown rather than gray (both useful characters for estimating hibernaculum age). Our observations indicate that some *L. a. floridensis* larvae apparently possess diapause capabilities. The observations at Everglades N. Pk. suggest differential responses to diapause inducing variables, since all life stages were found contemporaneously at the sites during the latter part of January, a time during the "dead of winter", when the ambient photophase is of shortest duration.

Some individuals of *L. a. floridensis* within a deme may begin to diapause by responding equally well to environmental combinations of photoperiod, temperature, and levels of relative humidity. [The induction of diapause is controlled mainly by photoperiod in all northern populations of *Limenitis* spp. (Clark & Platt 1969, Hong & Platt 1975)]. Such differences in diapause control mechanisms among insects have been described by Beck (1980) and Saunders (1982). Our field observations suggest that some *L. a. floridensis* fly all year long (contradicting Gerberg & Arnett 1989, who report that these insects only fly between April–Sept.).

Induction of diapause in second instar larvae of the temperate subspecies, *L. a. archippus* correlates with the appearance of the whitish, dorsal mid-abdominal saddlepatch on the young larvae. This saddlepatch overlies both the primordial gonads and paired ventrolateral neurosecretory ganglia. Platt (1989) presented evidence that this region of the larvae may be photosensitive, and that it influences both normal and abnormal development in northern populations of *L. a. archippus*. Southern populations of *L. a. floridensis* also possess larval saddlepatches, but the role of these saddlepatches remains unstudied.

TABLE 1. Records of 30 hibernacula of *L. a. floridensis* collected from northcentral and southwestern Florida during 1995–1996.

Date	Location	County	Hibernacula		
			Occupied	Empty	Observer
18–20/I/95	Corkscrew N. Park	Collier	3	0	D. Flaim
18–20/I/95	Everglades N. Park	Dade	2	0	D. Flaim
23/III/96	Newnan Lake Gainesville	Alachua	0	25	A. Platt

A well-documented intergrade zone exists between *L. a. archippus* and *L. a. floridensis* in northern Florida and southern Georgia (Remington 1958, 1968, Williams & Platt 1987, Ritland 1990, Ritland & Brower in review). Gene flow exists between these two subspecies throughout the Florida peninsula, and northward to Athens, Georgia, and the great Dismal Swamp in southeastern Virginia ( $36^\circ40'\text{N}$ ; Clark & Clark 1951). Alleles controlling facultative diapause may pass from these northern populations into more southern populations, and vice-versa.

It might be argued that the empty hibernacula we collected near Gainesville were those of *L. arthemis astyanax*, rather than belonging to *L. archippus floridensis*, since *L. arthemis astyanax* also occurs in Florida. However, five lines of evidence point strongly in favor of these hibernacula belonging to *L. a. floridensis*: 1) several authors (Kimball 1965, Gerberg & Arnett 1989, Platt & Maudsley 1994) report that *L. arthemis astyanax* is rare especially in southern Florida; 2) we identified all of the maturing larvae as being those of *L. a. floridensis* (although all North American *Limenitis* larvae are difficult to tell apart, especially in their early instars); 3) during the time of our observations, no adult or immature specimens of *L. arthemis astyanax* were sighted by us; 4) all of our observations were made in open marshy habitats typical for *L. a. floridensis*, but not for *L. arthemis astyanax*; and, finally 5) The empty hibernacula found near Gainesville all were of relatively large size (between 1.75–2.5 mm long), a further indication that they belonged to *L. archippus floridensis*.

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#### NOTES ON THE GENUS *STHENOPIS* (HEPIALIDAE) IN ALBERTA, CANADA

**Additional key words:** semivoltine, biennialism.

The nearctic genus *Sthenopsis* Packard (Hepialidae) currently contains five species (Davis 1983), of which *S. argenteomaculatus* (Harris), *S. purpurascens* (Packard) and *S. quadriguttatus* (Grote) purportedly occur in Alberta (Bowman 1951). Despite their large size and peculiar habits, little is known about their biology and specimens are rare in collections. The purpose of this note is to report on the adult biology and distribution of the genus in Alberta. *S. argenteomaculatus* does not occur in Alberta, and *S. quadriguttatus* was placed into synonymy with *S. purpurascens* by Nielsen et al. (1999) based on morphological characteristics. Our observations of sympatric populations of *S. purpurascens* and *S. quadriguttatus* color morphs support this view.

**Specimens examined and study sites.** A total of 96 *Sthenopsis* specimens from Alberta and Saskatchewan were examined, from the following sources: Northern Forestry Centre (NFC) (Canadian Forest Service, Edmonton), University of Alberta Strickland Museum (UASM) and the private collections of the authors.

Behavior observations and habitat notes were based on the following Alberta localities: Finnegan Ferry (51°8'N, 112°5'W), 15-July-1985 (DDL); Didsbury (51°40'N, 114°8'W), 23-July-1987 (BCS); 23 km N. of Lac La Biche (54°55'N, 112°05'W), 22-July-1997 (BCS); Rock Island Lake (55°35'N, 113°25'W), 26-July-1997 (BCS); Gregoire Lake Provincial Park (56°35'N, 111°10'W), 24-July-1997 (BCS); 10 km S Cooking Lake (53°21'N, 113°05'W), 28-31-July-1997 (DDL, BCS); Palisades Research Centre, Jasper National Park (52°58'N, 118°04'W) 1030 m, 8-July-1998 (BCS); Redwater Natural Area (53°55'N, 112°57'W), 28-July-1999 (BCS).

*Sthenopsis argenteomaculatus* occurs from Québec to New England, and westward to Minnesota and Ontario (Strecker 1893, Forbes 1923, Riette 1992, Handfield 1999). It is also reported from Alberta (Bowman 1951) and Saskatchewan (Hooper 1981), and Ives and Wong (1988) state this species occurs throughout the prairie provinces. However, this species has often been confused with *Sthenopsis purpurascens* (Forbes 1923), and specimens labeled as *S. argenteomaculatus* in the Bowman collection (UASM) and the NFC are variants of *S. purpurascens*. Hooper (1981) and Ives and Wong (1988) provide a figure of a specimen identified as *S. argenteomaculatus*. Comparisons with illustrations of *S. argenteomaculatus*

from eastern North America (Solomon 1995, Handfield 1999) and specimens from Nova Scotia (BCS) reveal that the figures in Hooper (1981) and Ives and Wong (1988) are actually *S. purpurascens*. Furthermore, the peak flight period of *S. argenteomaculatus* is in mid- to late June, whereas *S. purpurascens* has a much later peak, from mid-July to August (Handfield 1999). Hooper (1981) states that in Saskatchewan, "adults [of the Hepialidae] emerge from mid-July to September". Based on this, previous reports of *S. argenteomaculatus* for Alberta and Saskatchewan should be referred to *S. purpurascens*.

*Sthenopsis purpurascens* ranges from British Columbia and the Northwest Territories east to Labrador and New York (Grote 1864, Forbes 1923, Prentice 1965, Handfield 1999), and as far south as the White Mountains of Arizona in the west (D. Wagner pers. comm.). In Alberta, this species is most common throughout the boreal mixed wood and aspen parkland ecoregions, and occurs locally in the mountain and prairie regions. The boreal forest localities include a range of habitats; the Cooking Lake site consists of mature trembling aspen (*Populus tremuloides*) woods, with an understory of beaked hazelnut, *Corylus cornuta*, and wild red raspberry, *Rubus idaeus*. The Redwater site is sandy, open jack pine (*Pinus banksiana*) forest, interspersed with stands of trembling aspen and paper birch (*Betula papyrifera*). Green alder (*Alnus crispa*) is the most common understory shrub. The Palisades Research Centre locality is within the montane ecoregion (Strong & Leggat 1992), and consists of dry, open meadows with stands of trembling aspen and lodgepole pine (*Pinus contorta*). *S. purpurascens* also occurs in riparian balsam poplar (*Populus balsamifera*) groves in the mixed grass prairie ecoregion (Finnegan Ferry site); populations here are likely restricted to riparian areas, since the larvae bore in the roots of poplar and aspen, *Populus* spp. (Prentice 1965, Gross & Syme 1981). It appears that *S. purpurascens* occurs throughout most of the province where suitable host plants occur.

The light color form (formerly *Sthenopsis quadriguttatus*) occurred together with typical *S. purpurascens* at all 1997 localities, with the exception of Gregoire Lake P.P. The fact that both phenotypes were collected together at several sites suggests that the habitat requirements and phenology of the two phenotypes are very



similar, supporting the synonymy of *quadriguttatus* into *purpurascens* proposed by Nielsen et al. (1999). Furthermore, the two phenotypes are almost identical in wing pattern, shape and size; only the ground color varies. Similar morphs (with salmon or brown ground color) occur in *Hepialus behrensi* (Stretch) (D. Wagner pers. comm.) and *Gazorycta noviganna* (Barnes & Benjamin) (C. Schmidt unpubl. data).

The relative frequency of phenotypes in the specimens examined is unbiased in males (17 "*quadriguttatus*" : 15 "*purpurascens*";  $X^2 = 0.125$ ,  $0.50 < p < 0.75$ ) but a significantly higher proportion of females exhibited the *quadriguttatus* phenotype (46:18;  $X^2 = 12.25$ ,  $p < 0.001$ ). Assuming both phenotypes are equally likely to be attracted to light, it appears that the mechanisms determining phenotype may be sex-linked.

**Flight observations.** Male and female *Sthenopsis purpurascens* were observed flying at dusk; nightly flight activity was very brief, occurring between 2210 h and 2300 h (Cooking Lake and Redwater), with sunset at 2135 h (MST). Crepuscular flight activity is characteristic of hepialids, including other members of the genus *Sthenopsis* (Winn 1909, McCabe & Wagner 1989, Wagner & Rosovsky 1991). Females displayed a nearly stationary, hovering flight, usually less than one meter above the shrub understory. One female was observed ovipositing between 2245 h and 2300 h, while exhibiting this type of behavior (Redwater site). Eggs were broadcast over vegetation consisting of low, herbaceous plants and scattered aspen saplings and alder shrubs. Although it was difficult to determine the rate at which eggs were dropped, captive females can lay approximately 1.5 eggs per second.

Males were only rarely observed flying, and flight became rapid and erratic when disturbed. Members of the genus *Sthenopsis* are unusual in that males possess long-range sex attractants, whereas this strategy is usually characteristic of female Lepidoptera (Mallet 1984, Wagner & Rosovsky 1991). Two types of courtship behaviour have been observed in *Sthenopsis*: Males of *S. thule* and *S. argenteomaculatus* form mating swarms (leks) which females enter to mate (Winn 1909, Covell 1981), and male *S. auratus* are sessile and call for females, fanning their wings over the scent tufts (McCabe & Wagner 1989). These two mating strategies may be density-dependent, with male lekking behaviour occurring at higher densities (Wagner & Rosovsky 1991). Since our observations of *S. purpurascens* failed to turn up males exhibiting courtship behavior, it remains unclear which courtship type this species exhibits.

Female *S. purpurascens* are more likely to be collected, since there is a high female bias in examined specimens (64 ♀ : 32 ♂) and sex ratios are unbiased in the Hepialidae (Wagner & Rosovsky 1991). This is likely due to the fact that females have a longer nightly flight period during which oviposition occurs, while males are only active for a brief time period (D. Wagner pers. comm.). In hepialids where females release sex attractants, collections are often male-biased (Wagner & Rosovsky 1991).

**Phenology.** Data labels of examined specimens range from July 5th to August 14th, and indicate the peak flight occurs during the last two weeks of July. Larvae of *S. purpurascens* likely take two years to develop (Vallée & Béique 1979); this can result in adults being much more common in alternating years. Out of the 16 years represented by the specimens examined (between 1931 and 1999), only five are even-numbered years; this phenomenon has also been observed in other hepialids (Wagner et al. 1989). It is thought that biennial species remain synchronous through complex interactions with predators and parasitoids, abiotic catastrophes, and plant defense mechanisms (Mikkola & Kononenko 1989, Mikkola 1976, Wipking & Mengelkoch 1994). The odd-year biennialism in *S. purpurascens* is synchronous with other biennial Lepidoptera species in the west; many of the Yukon species of *Boloria* (Nymphalidae), *Erebia*, *Oeneis* (Satyridae) and *Xestia* (Noctuidae) have a greater adult abundance in odd-numbered years (Lafontaine & Wood 1997). This odd-year zone extends from Hudson Bay westward to Fennoscandia (Lafontaine & Wood 1997), but it is not known what causes synchrony between such a wide range of taxa.

Further research is needed to determine the courtship and

mating behavior of *S. purpurascens*, whether or not density-dependent lekking occurs, if there is a pre-dawn flight period, and to verify if both phenotypes interbreed.

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## TWO LARGE TROPICAL MOTHS (*THYSANIA ZENOBIA* (NOCTUIDAE) AND *COCYTUS ANTAEUS* (SPHINGIDAE)) COLONIZE THE GALAPAGOS ISLANDS

**Additional key words:** light traps, island colonization.

The arrival and establishment of a species on an isolated oceanic island is a relatively rare event. The likelihood of colonization depends on a variety of features of the species, including dispersal ability, availability of food (hostplants or prey) and ability to reproduce. In this note, I discuss two recent Galapagos records of tropical moths in the context of island colonization.

*Thysania zenobia* (Cramer) is a tropical migratory species which has been occasionally collected in the Holarctic region (Ferguson et al. 1991). Its life history is unknown, but legumes are considered probable larval foodplants (Covell 1984). Between 20 and 25 April 1996, three fresh males were collected in a Mercury vapor light trap near Asilo de la Paz, Floreana Island, at 338 m elevation. The trap was located at the border of the agricultural zone and native forest. In March 1997, I collected another specimen in a forest of the endemic composite, *Scaevola pedunculata* Hook at Los Gemelos, Santa Cruz island, at 580 m elevation, feeding in a bait trap (mixture of rotting fruit). The fresh condition of these specimens suggested that they were from a population extant on the island, rather than migrant. These Galapagos specimens are identical in wing pattern and size to series from continental United States reported by Covell (1984).

*Cocytus antaeus* (Drury) is one of the larger hawk-moths of the Neotropical region. Members of the Annonaceae have been reported as hostplants (Kimball 1965). Dyar (1901) and Matteson (1933) described its life cycle. I collected two specimens on Santa Cruz Island. On 26 May 1996, I captured a fresh female in a mercury vapor lamp trap at Media Luna (580 m elevation), the fresh condition again suggesting an existing population. This habitat is a mature forest of the endemic *Miconia robinsoniana* Cong. (Melastomataceae), native ferns and the introduced tree *Cinchona succirubra* Klotzsch (Rubiaceae). One month later, one worn male was collected by Godfrey Merlen at an outdoor fluorescent light at the Charles Darwin Research Station (sea level).

Although I have never collected larvae of this species, farmers in Santa Cruz and San Cristobal Islands have reported the presence of "voracious green hornworms" feeding on leaves and branches of the introduced custard apple (*Annona cherimola* Mill). It is likely that these reports refer to *C. antaeus*, because no other Galapagos sphingids feed on members of the Annonaceae.

The lack of specimens of these two moth species in previous lepidopteran surveys of the islands suggests that these are relatively recent additions to the fauna. Hayes (1975) did not report their presence in the archipelago but his species list was based on specimens collected by early expeditions with less efficient light traps

(kerosene lamps) and collections made by amateur entomologists. Recently (1989 and 1992), Bernard Landry carried out an intensive Lepidoptera survey on the islands but he never collected the species (Landry pers. comm.). However, it is also possible that the absence of these species from earlier collections is due to flight time. I trapped both species late at night (2300 h to 2400 h) and few collections have been made during these hours by earlier collectors.

Several features of the biology of these two species may have contributed to their ability to reach the Galapagos. Both, *C. antaeus* and *T. zenobia* have a history of long dispersal events by active flying to new areas, including oceanic islands (Ferguson et al. 1991, Schreiber 1978). The occurrence of many species of Annonaceae, all of which were introduced by humans in the present century (Lawesson et al. 1987), has probably favored the establishment of *C. antaeus*.

Although the hostplant of *T. zenobia* is unknown legumes are a likely candidate (Covell 1984). There are many species of legumes on the Galapagos islands, including native and endemic species, and one of these could provide a suitable hostplant.

I suggest that many of the macrolepidoptera that have colonized the Galapagos arrived by natural means and not as a direct result of human activity. However, their establishment has been facilitated by the increase in the number of introduced plant species, deforestation and other human-related activities.

Voucher specimens have been deposited in the entomological collection of the Charles Darwin Research Station Museum on Isla Santa Cruz, Galapagos.

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#### AN ANTI-PREDATOR BEHAVIOR IN LARVAE OF *LIBYTHEANA CARINENTA* (NYMPHALIDAE, LIBYTHEINAE)

**Additional key words:** ant-predation, *Celtis*, frass chains.

Strategies of avoiding predators are well documented in larvae of Lepidoptera, and include a variety of morphological, chemical and behavioral traits (Malicky 1970, Brower 1984, Heads & Lawton 1985, Stamp & Casey 1993, Freitas & Oliveira 1992, 1996, Loeffler 1996). One rather unusual behavioral defense found in larvae of species of Charaxinae and Limenitidinae is the construction of frass chains (DeVries 1987, Freitas & Oliveira 1996). Frass chains are stick-like structures formed by fecula and silk where the larvae rest when not feeding, and provide an efficient refuge against predation by "walking" arthropod predators by isolating the larvae from the leaf blade when not feeding (Freitas & Oliveira 1996). In this note, a similar behavior is reported in larvae of the Libytheinae *Libytheana carinenta* (Cr.) at two sites in southeastern Brazil.

Field observations were conducted in two fragments of deciduous forests in São Paulo state; the "Fazenda Três Barras", in Castilho, in February 1995 and in the "Reserva da Mata Santa Genebra", Campinas, in March 1997, March–April 1998 and March–April 1999. The larvae were observed feeding on *Celtis iguanae* (Ulmaceae) in Castilho, and on *C. spinosa* in Campinas.

Larvae of *Libytheana carinenta* were observed resting on the midvein of partially eaten leaves of *Celtis* spp. (Fig. 1). This behavior was observed in all instars, being present even in fully grown fifth instar larvae. Most of the observed eggs ( $n > 50$ ) were laid individually on very young leaves (with five observations of eggs on spines on the shoot tips), and larvae start to eat alongside the central vein just after hatching, resulting in the formation of the stick-like structure on the expanding leaf. Larvae rest on the tip of this structure, returning to the leaf blade only for eating. No larvae of *L. carinenta* were observed feeding asymmetrically on the leaf tip, or on only one side of the leaf.

Although *Celtis spinosa* does not bear extrafloral nectaries, ants were frequently seen on branches and leaves of *Celtis* spp. in forest edges. In this habitat ants commonly associate with Homoptera, especially on shoot tips, and were observed preying on small moth caterpillars, suggesting that they could be effective predators of butterfly larvae as well. As also recorded by Freitas and Oliveira (1996) for another ant-butterfly interaction, these and other ants were never observed climbing onto *L. carinenta*'s stick-like

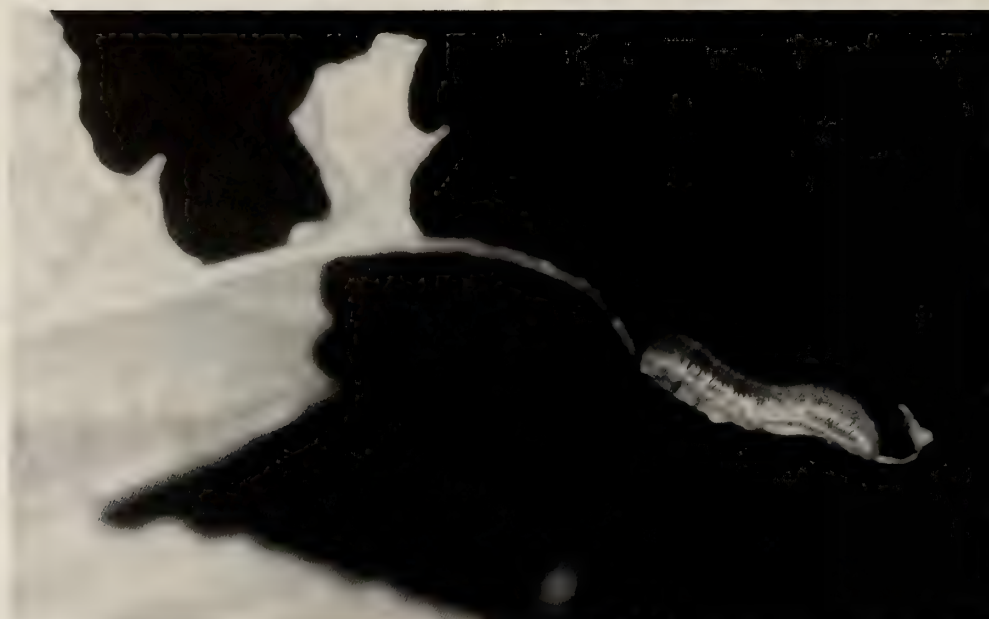


Fig. 1. Third instar larva of *Libytheana carinenta* resting in the remaining central vein of a *Celtis spinosa* leaf.

structures. Therefore the behavior of constructing and resting on these structures may provide a refuge against ant predation on the host plant, and in this way could be analogous to the behavior of resting on frass chains, observed in the Eurytelinae, Charaxinae and Heliconiinae.

Considering Libytheinae as the most basal lineage of Nymphalidae (Harvey 1991), the results presented here could be important to the understanding of the anti-predator strategies present in other Nymphalidae. For example, in the Limenitidinae different degrees of complexity of similar refuges are known, ranging from the simple remaining midvein (as described in the present paper) to true frass chains, with several known variations (Morrell 1954, Fukuda et al. 1972).

Data on larval biology of Libytheinae are scarce, and no defensive strategies have been reported, making this the first report of a defensive behavior in Libytheinae larvae. Similar simple structures are present in larvae of several moth species in different areas of tropical forests in Brazil, as well as in the pierid genus *Dismorphia* (Brown 1992), and in some Heliconiini, that construct or leave island-like structures on leaf edges (Benson et al. 1975) which were considered to be analogous to the frass-chains (see discussion in Freitas & Oliveira 1996). All these behaviors represent different ways for the larvae to maintain themselves isolated from the leaf blade; their occurrence in several different lineages of Lepidoptera shows that the fixation of this trait in many cases could be explained by predation pressure.

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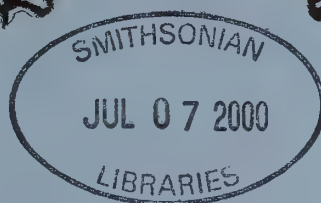
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**Cover illustration:** Adult of the tiger swallowtail, *Papilio glaucus* (Papilionidae). Pen and ink drawing by Deane Bowers, University of Colorado.

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## DISTRIBUTION AND HOSTPLANT RECORDS FOR *EUPACKARDIA CALLETA* FROM SOUTHEASTERN TEXAS WITH NOTES ON MANDIBULAR MORPHOLOGY OF ATTACINI (SATURNIIDAE)

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**ABSTRACT.** *Eupackardia calleta* (Westwood) is recorded on privet (*Ligustrum*) from Kingwood, Texas. This new county record represents a northeastern range extension of 100 miles and confirms privet as a hostplant under natural conditions. The role of the mandible in digestion of the hostplant is discussed.

The last instar larval mandible of most Attacini either lacks teeth or has the cutting edge bluntly serrated with reduced teeth. In contrast, the distinctive mandible of *E. calleta* contains three large teeth and deep molar ridges, an autapomorphy for the genus. Well-developed mandibular teeth are present on the last instar of a few unrelated Saturniinae and Ceratocampinae; therefore this character is homoplastic in Saturniidae. A structurally complex mandible of the "sphingid-type" occurs in several saturniids such as *Antheraea pernyi* (Guér.- Mén.) (Saturniidae). This mandible type is illustrated.

There are two ontogenetic patterns of mandibular development in Saturniidae. In one case, teeth are present in the first instar, then lost in later molts. The mandibular development of *E. calleta* represents an alternative scenario where teeth are present throughout the larval stage.

**Additional key words:** *Ligustrum*, ontogenetic development, Sphingidae, Notodontidae.

*Eupackardia calleta* (Westwood) is a member of the Attacini, usually considered the sister group to *Rothschildia* (Ferguson 1972, Peigler 1989, Friedlander et al. 1998). This species is distributed from Central America (Honduras, Guatemala) north to Arizona and southern Texas (Victoria Co., Calhoun Co.) (Ferguson 1972, Wolfe 1995, Tuskes et al. 1996). The systematics and biology of *E. calleta* have been reviewed by several authors including Ferguson (1972), Weast (1989), Miller (1976), Lemaire (1978), and Tuskes et al. (1996).

Weast (1989) suggested that systematic studies of *E. calleta* are needed. Tuskes et al. (1996) illustrated three larval forms of the United States populations, but did not study their mandibular morphology. In this paper we present biological data on *E. calleta* from southeastern Texas, then compare the mandibular

morphology to other Attacini, with emphasis on related nearctic taxa. Ontogenetic and phylogenetic observations are also included.

### MATERIALS AND METHODS

In order to survey saturniid mandibles, preserved larval specimens or exuviae associated with cocoons and emerged adults were taken from the authors' collection and dissected. The mandible was either slide mounted in Euperal or preserved in alcohol. For analysis with a J.O.E.L. JSM 820 scanning electron microscope, each sample was attached to a stub with carbon paint and coated with a thin conductive layer of gold-palladium. Mandibular terminology is based on Godfrey (1972).

**Material examined:** *Eupackardia calleta*: TEXAS (various localities, ex ova from female moths in lab culture): 10 eggs, 10 first instars, 27 second to fourth in-

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TABLE 1. Mandibular morphology of selected late instar Attacini larvae occurring in the Western Hemisphere. Locality data designate source of the study specimens.

Species examined	Source	Cutting edge of mandible
<i>Callosamia angulifera</i> (Wlk.)	USA	Teeth reduced, margin bluntly serrate
<i>Callosamia promethea</i> (Drury)	USA	Teeth reduced, margin bluntly serrate
<i>Callosamia securifera</i> (Maas.)	USA	Teeth reduced, margin bluntly serrate
<i>Eupackardia calleta</i> (Ww.)	Texas, Mexico	Teeth present, well-developed
<i>Hyalophora cecropia</i> (L.)	USA	Teeth absent
<i>Hyalophora columbia</i> (S. I. Smith)	USA	Teeth absent
<i>Hyalophora euryalus</i> (Bdv.)	USA	Teeth reduced, margin bluntly serrate
<i>Hyalophora gloveri</i> (Stkr.)	USA	Teeth reduced, margin bluntly serrate
Prob. <i>Rothschildia cincta</i> (Tepp.)	Prob. Baja California	Teeth reduced, margin bluntly serrate
<i>Rothschildia erycina</i> (Shaw)	USA	Teeth reduced, margin bluntly serrate
<i>Rothschildia forbesi</i> Benj.	Texas	Teeth absent
<i>Rothschildia lebeau</i> (Guér.-Mén.)	Honduras	Teeth absent
<i>Rothschildia orizaba</i> (Ww.)	Ecuador	Teeth reduced, margin bluntly serrate
<i>Samia cynthia</i> (Drury)	USA	Teeth reduced, margin bluntly serrate

stars, 6 pupal cases (with larval exuviae), det. V. A. Passoa, mandible slides #581, 582 S. Passoa collection; Harris Co., Kingwood, XII-1995, on *Ligustrum*, V. A. Passoa, 6 mature larvae, det. V. A. and S. Passoa, mandible slide # 616 S. Passoa coll.

MEXICO: various localities, collection data unknown, 2 first instars, 18 second to fourth instars, 3 pupal cases (with larval exuviae), det. V. A. Passoa; Mich. [Michoacan], Uruapan (sic) [Uruapan], 2-X-1941, coll. [D. M.] Delong, det. V. A. and S. Passoa (1 last instar larva with mandibles slide mounted (The Ohio State University collection).

One to ten mandibular pairs of each species (Table 1) were examined, depending on material available.

#### RESULTS AND DISCUSSION

During November 1995, the senior author collected seven third instar larvae of *E. calleta* on privet (*Ligustrum*) from her backyard in Kingwood, Harris Co., Texas. This is a northeastern range extension of approximately 100 miles (161 km) and a new county record. It remains to be determined if *E. calleta* is now established in Harris County.

Tuskes et al. (1996) considered *Leucophyllum frutescens* (ceniza, purple sage) to be the main host-plant for *E. calleta* in Texas. Privet is normally treated

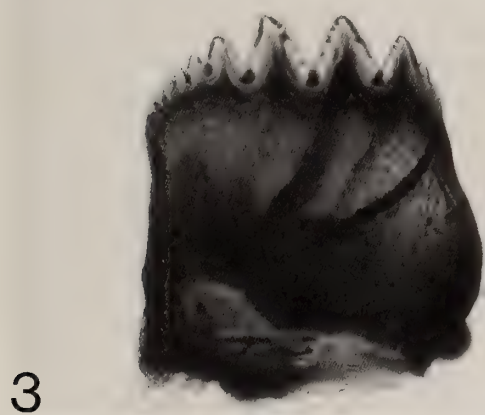
as an artificial laboratory host (Ferguson 1972, Tuskes et al. 1996). Ours is the second published record for *E. calleta* eating ornamental privet under natural conditions, supporting the suggestion of Weast (1989) that privet is an important hostplant of this species near urban areas of Texas. In fact, *E. calleta* appears to be oligophagous on several genera of Oleaceae, including privet in Texas (present study) and Mexico (Peigler pers. comm.), *Fraxinus greggii* A. Gray in western Texas (Peigler pers. comm.), and *Forestiera angustifolia* Torrey (Stone 1991). A mature larva of *E. calleta* on privet from Kingwood, Texas, is illustrated in Fig. 1. At maturity, the larva lacks long and dark scoli which are characteristic of earlier instars (Fig. 2). In spite of the availability of ceniza nearby, *E. calleta* was found only on privet in the senior author's backyard.

Examination of *E. calleta* mandibles from Texas showed that these structures are atypical compared to other saturniids described in the literature. Bernays and Janzen (1988) characterized late instar saturniid mandibles as "short, with a broad base, and without obvious teeth". This definition does not fit *E. calleta* which has large teeth in both the early (Fig. 3) and last instars (Figs. 4, 5, and 6).

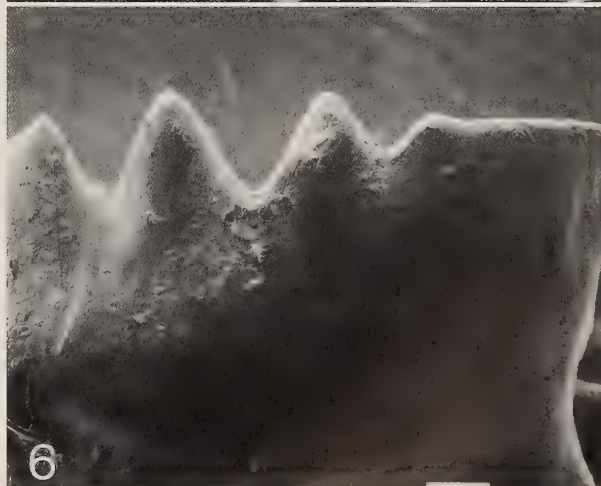
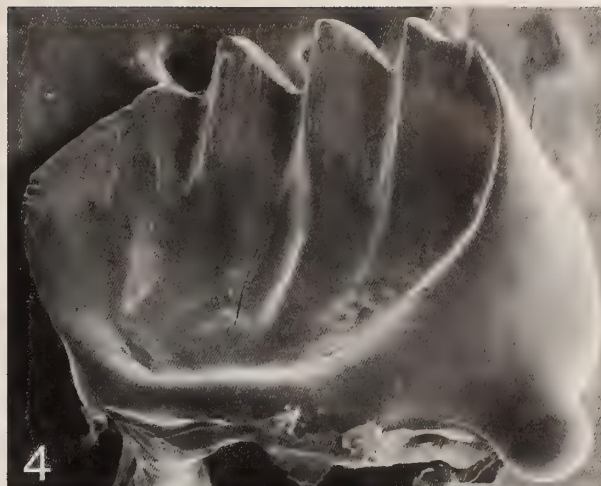
Except for *E. calleta*, members of the Attacini typically lack well-developed mandibular teeth in the last instar or have the cutting edge of the mandible serrated with blunt lobes (Table 1). Mandibular teeth are also absent in mature larvae of two Indo-Australian Attacini, *Attacus atlas* (L.) (Heppner et al. 1989) and *Coscinocera hercules* (Miskin) (specimens in Passoa collection).

Our data on saturniid mandibles agree with results of a survey of notodontid mandibles published by Godfrey et al. (1989) in several respects. Last instar mandibles of the Notodontidae usually lack teeth, except for a few apparently unrelated exceptions. This is also true in Saturniidae. Outside of the Attacini, mature larvae of *Actias selene* (Hbn.), *A. luna* (L.), *Argema mittrei* (Guér.-Mén.) (Saturniinae) and *Citheronia regalis* (F.) (Ceratocampinae) (specimens in Passoa collection) have well-developed mandibular teeth, so the presence of teeth on saturniid mandibles is homoplastic across several subfamilies.

Large teeth also occur in the *Antheraea* genus complex, for example, *Antheraea pernyi* (Guér.-Mén.) and its purported synonym *A. hartii* (Moore), *A. polyphemus* (Cram.), and *Opodiphthera eucalypti* (Scott) (spms. in Passoa coll.). In addition, the mandible of *A. pernyi* is unusual because it matches the "sphingid-type" as defined by Bernays and Janzen (1988). Sphingid mandibles were characterized as being "ridged in a

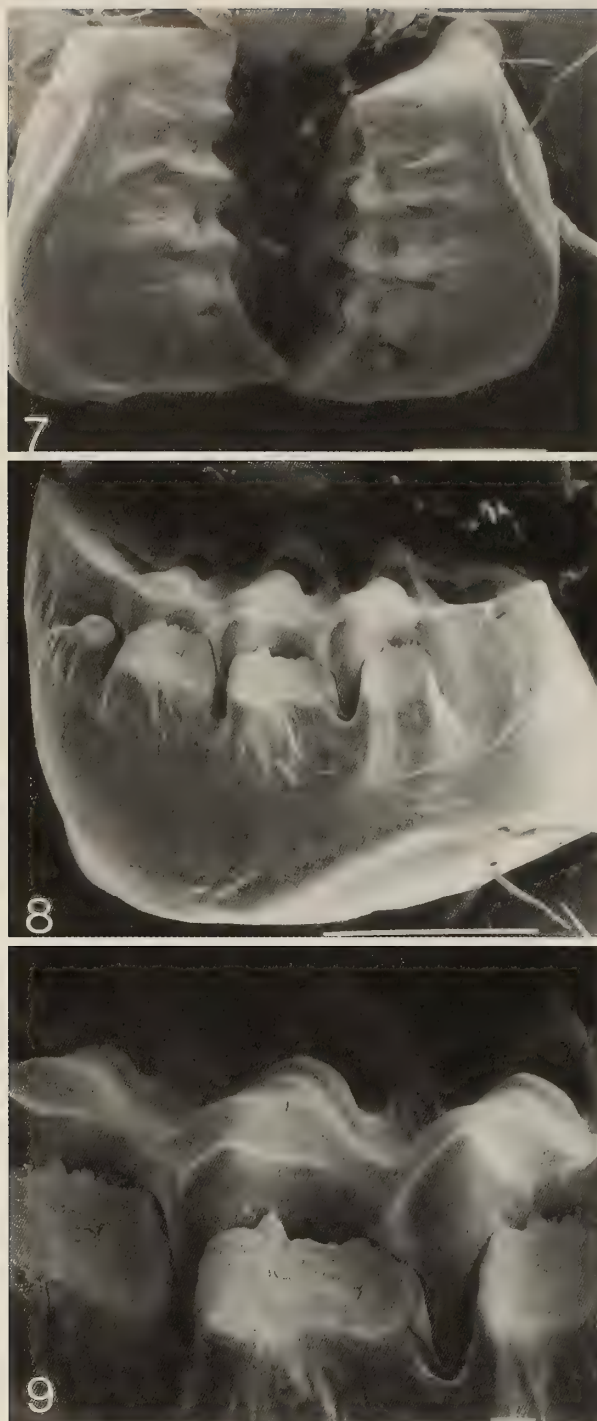


FIGS. 1-3. *Eupackardia calleta* (Westwood) from Texas. 1, late instar larva on privet (lateral view). 2, mid-instar larva on privet (dorsal view). 3, early instar mandible, oral surface, ventral view, photographs under polarized light, 100 $\times$ .



FIGS. 4-6. Mandible of last instar *Eupackardia calleta* (Westwood), scale line = .10 mm in all figures. 4, oral surface, ventral view, 70 $\times$ . 5, teeth and deep molar ridges, ventral view, 150 $\times$ . 6, teeth on cutting margin, dorsal view, 95 $\times$ .





FIGS. 7-9. Mandible of last instar *Antheraea pernyi* (Guér.-Mén.). 7, complex pattern of teeth on dorsal and oral surfaces, ventral view, 27 $\times$ , scale line = 1 mm. 8, overlapping teeth of dorsal surface, ventral view, 33 $\times$ , scale line = 1 mm. 9, tooth of dorsal surface, ventral view, 70 $\times$ , scale line = .1 mm.

variety of complex ways". The mandible of *A. pernyi* (Figs. 7, 8, and 9) has a series of complex ridges on the dorsal surface that appear to form overlapping teeth, in addition to several smaller toothlike projections on the oral surface. The mandibles of *E. calleta* and *A. pernyi* suggest it is wiser to characterize saturniid mouthparts with ecological or physiological criteria (cutting versus grinding), instead of using a phylogenetic approach at the family level as did Bernays and Janzen (1988) in their study of saturniid and sphingid mandibles.

There appear to be two ontogenetic patterns for saturniid mandibles. In one pattern, first instar larval mandibles have teeth; subsequently these teeth are lost in later molts. This pattern is typical for Costa Rican saturniid species in four subfamilies (Bernays & Janzen 1988). A second pattern is found in *E. calleta* where early instars have mandibular teeth (Fig. 3) that are retained throughout larval life (Figs. 4, 5, and 6). This dichotomy was also noted by Godfrey et al. (1989) in notodontid genera.

Godfrey et al. (1989) stated that characterization of certain taxa by mandibular morphology was "problematical" because in some species the mandibular margin was intermediate between toothed and smooth. Intermediate conditions are common with Saturniidae, as shown in Table 1 by the term "margin bluntly serrate". A bluntly serrated mandible has round conical projections that resemble small teeth, or an irregular mandibular margin with indentations. *Callosamia* is an example of the first condition where from 10-15 small teeth cover the cutting margin of the mandible.

Irregular mandibular margins are found in *Hyalophora* and *Rothschildia* where it is difficult to discern teeth, but the mandibular margin is not straight. Dockter (1993) warned that mandibular wear must be taken into account when describing mandibles. It is unclear whether bluntly serrated teeth in Saturniidae are a transition state between toothed and smooth mandibles, as noted by Godfrey et al. (1989) in notodontids, or instead represent worn mandibular teeth as described by Dockter (1993) in *Heterocampa* and Sourakov (1996) in larvae of satyrid butterflies. Examination of unworn mandibles on freshly molted larvae are needed to resolve this question. Thus, it may be premature to characterize saturniid mandibles as usually toothless (Bernays & Janzen 1988) until more ontogenetic studies are published.

In summary, the mandibular shape of Macrolepidoptera depends on several factors including head size and food toughness (Bernays 1986), food particle size and chemistry (Bernays & Janzen 1988), the need to pierce the chorion of the egg at eclosion, and a need to

seal the oral cavity during ingestion (Godfrey et al. 1989). Unlike notodontids which use toothed mandibles to pierce the leaf epidermis (Dockter 1993), *E. calleta* does not skeletonize leaves during any instar (V. A. Passoa pers. obs.). Therefore, it seems likely that a toothed mandible is required for other reasons.

Bernays and Janzen (1988) noted that larvae which feed on toxic plants tend to be associated with mandibles that contain teeth. They (Bernays & Janzen 1988) suggested that complete mastication of the leaf tissue allows more complete digestion, a strategy not possible with hostplants containing tannins that inhibit digestive efficiency. However, the digestive physiology of *E. calleta* may be more complicated than other Saturniidae. Caterpillars of *E. calleta* secrete a pungent liquid containing phenolic compounds and biogenic amines from their scoli when disturbed, but it is unknown if plant toxins are sequestered for this secretion (Deml & Dettner 1993). Until the metabolism and defensive chemistry of *E. calleta* are clarified, it may be premature to assume mandibular teeth are an aid to coping with plant toxins. Nevertheless, *E. calleta* larvae do utilize toxic plants (Weast 1989).

Besides the need to understand mandibular morphology in an ecological context, it should be noted that a survey of saturniid mandibles would aid identification of the immatures. Minet (1994:70) mentioned mandibular secondary setae as an apomorphy of the Lasiocampidae, although these setae are also independently evolved in other macrolepidopteran families. Mandibular secondary setae are present (*Agapema*) or absent (*E. calleta*) in Saturniidae, thus this character has potential for identification purposes. Mandibular teeth associated with the cast larval exuvium can be used to separate cocoons of *E. calleta* (teeth present) and *Rothschildia* (teeth absent). Both genera are easily confused due to their similar pupal morphology. A final example is *A. luna* and *A. polyphemus*. Although these genera are often confused as larvae (Ferguson 1972:207), their mandibles are completely different, being either simple and toothed (*A. luna*) or complex with ridges (*A. polyphemus*). More descriptive studies of saturniid mandibles will no doubt yield further examples.

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Voucher specimens of *E. calleta* and its hostplant are deposited in The Ohio State University's Insect Collection and Herbarium.

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## METHOD OF HANDLING AFFECTS POST-CAPTURE ENCOUNTER PROBABILITIES IN MALE *HYPOLIMNAS BOLINA* (L.) (NYMPHALIDAE)

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**ABSTRACT.** Mark-recapture studies of butterfly populations are often plagued by low recapture rates, which make population estimation problematic. One reason for low recaptures is that the handling process of capture, marking and release contributes to low and unequal catchability of marked individuals. Here we report the results of an experiment conducted to evaluate the hypothesis that cooling individuals prior to release minimizes handling effects. The post-capture difference in site fidelity of territorial male *Hypolimnas bolina* (L.) (Lepidoptera: Nymphalidae) was compared among three groups: (1) males handled normally, (2) males chilled prior to release, and (3) uncaught controls. Unchilled males showed significantly reduced site fidelity compared to both control and chilled butterflies. Furthermore, chilled butterflies resumed activity after capture in a manner similar to uncaught controls. These results indicate that chilling has the potential to minimize the adverse effects of handling on subsequent butterfly catchability. Since 'equal catchability' of caught and uncaught individuals is a critical assumption of mark-release-recapture programs, this method has the potential to greatly increase the accuracy of subsequent population estimates. On this basis, in population studies on butterflies, the precise method of handling may prove a more meaningful consideration than the question of whether or not to handle.

**Additional key words:** catchability, mark-release-recapture, censusing, population estimation.

Mark-recapture methods represent a powerful tool for the estimation of animal population parameters, especially those of invertebrates (Seber 1973, Southwood 1978, Begon 1979). These methodologies have often been applied to the study of butterfly populations; however, on many occasions, such programs are plagued by low recapture rates, sometimes in the order of 1 to 10% (Brussard & Ehrlich 1970, Urquhart et al. 1970, Cook et al. 1971, Urquhart & Urquhart 1976, Watt et al. 1977, Cullenward et al. 1979). This makes the estimation of population size and related measures problematic (Rosenberg et al. 1995), and researchers must often resort to less powerful methods, such as transect-based surveys to census their populations (e.g., Pollard 1977, Eberhardt 1978, Thomas 1983, Dent 1997).

One of the many potential causes of low recapture rates in the Lepidoptera is that the actual process of capture and handling may affect the behaviour of marked individuals, reducing their chance of being recaptured (Gall 1984). This effect would contribute to low catchability in marked individuals, and lead to significant bias in subsequent population estimates (Gall 1984, Rosenberg et al. 1995). Although crucial to the application of mark-recapture methods, few authors attempt to validate the assumption of 'equal catchability' (Gall 1984). Several attempts to assay the effects of capture in butterflies have indicated that the capture and handling process may have strongly negative effects on subsequent catchability (Singer & Wedlake 1981, Lederhouse 1982, Morton 1984).

In recent times, many workers have taken to cooling individuals before their release (e.g., Bull et al. 1985, Zalucki & Kitching 1985, Suzuki & Zalucki 1986, Rutowski 1992, Zalucki 1993, Wickman & Jansson 1997). This technique stems from the idea that increased immobilization of individuals immediately prior to their release helps to reduce their subsequent degree of 'panic' (Wickman & Jansson 1997). In this way, individuals are supposedly more likely to remain in the immediate study area and behave normally, rather than disperse and avoid further capture (as found by Lederhouse 1982). The use of this technique, however, is based on mostly anecdotal information, and little, if any, published research has been conducted to evaluate its merit.

The aim of this paper is to evaluate the hypothesis that cooling individuals prior to release may increase their subsequent catchability relative to individuals handled in the normal manner. This hypothesis is investigated using territorial mate-locating males of the nymphalid species *Hypolimnas bolina* (L.).

### MATERIALS AND METHODS

Male *H. bolina* in resident territories were censused along a 1020 m transect (Rutowski 1992) located on campus at James Cook University in Townsville, Australia (19°15'S, 146°45'E). Sampling was conducted in two rounds in 1998; from 9–12 February and 16–19 April, and once in 1999; from 22–25 February 1999. On each sample round, transects were censused

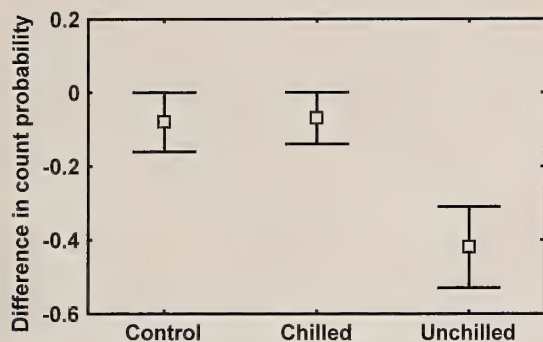


FIG. 1. The average ( $\pm$  SE) difference in the probability of encountering a male *H. bolina* between pre- and post-capture censuses, as a function of which treatment group he was assigned to. Control males were not caught, chilled males were caught and cooled before release, and unchilled males were caught but not chilled.

hourly for the first two days to identify individuals of high territory site fidelity (for census techniques see Pollard 1977). Notes on size and wing wear were taken to allow reliable identification of these individuals in subsequent censuses (Rutowski 1992). At 1000 h on the third day (termed the marking round), each resident was randomly assigned to one of three treatment groups. 'Unchilled' males were captured at their site, marked with an identification number on both hind-wing undersides, and released immediately (total handling time of 40–50 seconds). 'Chilled' males were similarly captured and marked, but were held for a further 210 seconds in a paper envelope placed on a block of ice wrapped in newspaper (Wickman & Jansson 1997), then released directly back to their perch. Notes were taken on the immediate behavior of individuals in these two treatments upon release. Butterflies of the third group, designated as control, were not caught. Hourly transects were then conducted for the remainder of the third day and the next day to determine the behavior of males in all three groups. Censuses were conducted no sooner than 0900 h and no later than 1500 h, and only in the presence of sunshine before and during the entire transect. This was done to ensure that individuals were censused only at times of maximum site fidelity. During the course of each transect, individual males were deemed re-counted if they were within 20 meters of their designated territory, and actively engaged in defense of that site. No effort was made to search for individuals that were not immediately obvious at their sites following marking, hence the observation technique was kept similar before and after marking.

An index of site fidelity was calculated for each male by dividing his total counts by his total number of

count opportunities (i.e. the number of times his territory was passed during transect censuses). Since the ratio of before: after-marking counts in each treatment group was homogenous between sampling rounds (Chi-squared homogeneity test on before- and after-counts across the three rounds:  $\chi^2_2 < 2.79$ ,  $p > 0.24$  for each group), data were pooled across all rounds. Initially, pre- and post-marking round count probabilities were compared for control group butterflies only. This was done to check that the activity of untreated butterflies was homogenous and that no other factor, for instance weather, affected the probability of counting butterflies between censuses. Mean differences (pre- and post marking round) in count probabilities between butterflies of each treatment group were then compared using a one-way analysis of variance (ANOVA). Three comparisons were planned prior to analysis; these were (1) between chilled and unchilled butterflies, (2) between chilled and control group butterflies, and (3) between unchilled and control group butterflies. These contrasts were evaluated using least significant difference (LSD) test for planned, non-orthogonal comparisons (Sokal & Rohlf 1995). Prior to conducting analyses, data sets were transformed using the angular transformation, and Kolmogorov-Smirnov goodness of fit tests were used to confirm that the transformed data were normally distributed (Kolmogorov-Smirnov  $d < 0.24$ ,  $p > 0.20$  for all groups). Levene tests were used to check homoscedasticity among ANOVA groups; these were non-significant in all cases ( $p > 0.175$ ), which confirmed that data were homoscedastic. Two-tailed probabilities were used, and sample means throughout this paper are given  $\pm 1$  standard error.

## RESULTS

A total of 30 primary territory residents were identified during the three sampling occasions, and these were randomly distributed amongst treatments as follows: 11 chilled, 11 unchilled, and eight control. Of the total 226 count opportunities before the marking round, 191 counts were registered, and primary residents exhibited a mean site fidelity of  $0.87 \pm 0.02$  (each being present on approximately 87% of all count opportunities). Mean pre-marking site fidelity did not differ significantly among the three butterfly groups (control, chilled, unchilled; ANOVA on angular-transformed data,  $F_{2,27} = 0.15$ ,  $p = 0.86$ ). In addition, the mean site fidelity of control group butterflies was not significantly different between pre- and post-marking censuses (paired  $t$ -test on angular-transformed data,  $t = 0.63$ ,  $df = 7$ ,  $p = 0.55$ ).

Post-marking censuses revealed that four marked individuals (one chilled and three unchilled) had de-



served their territories. All other males were counted at least once defending their pre-designated territory area. The mean difference between pre- and post-marking round fidelity varied significantly among treatment groups (ANOVA on angular-transformed data,  $F_{2,27} = 3.97$ ,  $p < 0.05$ ; Fig. 1). Fidelity was reduced to a varying degree in all groups following the marking round. The reduction in site fidelity of unchilled butterflies was significantly greater than that of either control or chilled group butterflies (LSD test for planned comparisons,  $p < 0.05$ ). The significant difference between the two captured treatment groups demonstrated an effect due to the method of handling individual males before their release. Furthermore, the change in fidelity among chilled butterflies did not differ significantly from that shown by control group butterflies (LSD test,  $p = 0.85$ ). Hence, relative to uncaught controls, the process of capture and marking had no appreciable effect on the subsequent territorial fidelity of butterflies that were chilled prior to their release.

Captured and marked butterflies in each treatment group showed clear behavioral differences following their release. While all chilled males remained perched on the substrate where they were placed, non-chilled males either resumed active territory defense (2 males), roosted on the underside of shaded foliage near the site (2 males), or flew quickly out of the area (7 males). Hence, while all chilled butterflies remained in the vicinity of their territory (i.e., less than 20 meters away) in the first instance, only 4 (36.4%) of the 11 non-chilled butterflies did so.

#### DISCUSSION

Although based on relatively small sample sizes, the results of this experiment clearly support the hypothesis that cooling may reduce capture effects and increase post-handling catchability of territorial male *H. bolina*. Not only did the process of chilling affect the probability of resighting captured males, but chilled males also resumed activity in a manner similar to that of butterflies that were never caught. This result is significant, since it shows that chilling may not simply reduce or 'manage' the adverse effect of handling, but that this process has the potential to actually nullify short-term effects of capture. To our knowledge, this has not been demonstrated previously for any butterfly species.

These results contrast with the generally negative effects of handling of butterflies obtained in previous studies, for example Singer and Wedlake (1981), Lederhouse (1982), and Morton (1984). In these studies, however, no reference is given to any method of chill-

ing butterflies prior to their release, and it must be assumed that butterflies were simply released immediately following marking. The experiment conducted here on *H. bolina* corroborates the finding that butterflies handled in this manner may be less likely to be recaptured, but that this adverse handling effect may be mediated by a chilling treatment prior to release.

One concern with capturing and marking butterflies is that individuals will suffer from an increased level of predation owing to the wing mark and subsequent loss of crypsis or aposematism (Gall 1984, Reynolds et al. 1997). If present, such an effect is often difficult to distinguish from any potential effects arising from capture and handling. Fortunately, in this study, the contrasting results between treatment groups allowed the separation of specific marking effects. Since both treatment groups were given similar marks, chilled males provided an adequate control for the effects of wing marks in the unchilled group. That only the unchilled group of butterflies were less likely to be recounted than controls clearly suggests that, at least in the short term, these were affected by the method of handling and not by the marks placed upon their wings. A similar conclusion was reached by Morton (1984), who found that colored wing marks did not significantly affect recapture of the highly cryptic woodland butterfly *Melanargia galathea* (L.). The limitation with the current experiment, however, is that post-marking site fidelity was only measured for a period of two days. On this basis, the presence of a longer term effect due to wing marks in *H. bolina* cannot be completely discounted.

The question of why captured butterflies may be less likely to be resighted is not specifically addressed by this study, but some insight is afforded by casual behavioral observations made on released individuals. Clear differences in behavior were evident between treatment groups, and this resulted in more unchilled butterflies leaving their immediate area of capture in the short term. This difference alone may be responsible for differences in encounter probabilities of unchilled and chilled individuals, especially in the case of a site-tenacious butterfly such as male *H. bolina* (Rutowski 1992). In unchilled *H. bolina*, the decision to leave the territory is more likely to be made as a consequence of immediate 'panic' upon release. This behavior appears similar to the defensive or evasive response of butterflies to failed predatory attacks, or failed capture attempts. Chilled butterflies, however, remain in their territory area for quite some time whilst warming up, and therefore any active decision to abandon the site must be made at some later stage. On average, the difference between groups after



marking is that unchilled butterflies must decide whether to return to their former territory, and the chilled butterflies must decide whether to leave. If both these decisions are sufficiently unlikely, then discrepancies will exist between the recounts of chilled and unchilled group individuals, leading to the results observed in this study.

In theory (depending on specific post-capture behavioural responses), this principle may hold for a wide variety of butterfly species being sampled in a wide variety of circumstances. Indeed, both Lederhouse (1982) and Singer and Wedlake (1981) suggested that initial dispersal or displacement from the site of capture may have accounted for their observed capture effects in butterflies handled without chilling. The advantages of chilling may therefore lie in the prevention of early dispersal immediately following capture, as implied by Wickman and Jansson (1997). Since 'equal catchability' of caught and uncaught individuals is a critical assumption of mark-release-recapture programs, this method has the potential to greatly increase the accuracy of subsequent population estimates. On this basis, in studies that intend to employ mark-release-recapture techniques, the actual method of handling may prove a more meaningful consideration than the question of whether or not to handle.

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EARLY STAGES OF *CALIGO ILLIONEUS* AND *C. IDOMENEUS*  
(NYMPHALIDAE, BRASSOLINAE) FROM PANAMA, WITH REMARKS ON LARVAL  
FOOD PLANTS FOR THE SUBFAMILY.

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**ABSTRACT.** Here we describe the complete life cycle of *Caligo illioneus oberon* Butler and the mature larva and pupa of *C. idomeneus* (L.). The mature larva and pupa of each species are illustrated. We also provide a compilation of host records for members of the Brassolinae and briefly address the interaction between these butterflies and their larval food plants.

**Additional key words:** Central America, host records, monocotyledonous plants, larval food plants.

The nymphalid subfamily Brassolinae includes Neotropical species of large body size and crepuscular habits, both as caterpillars and adults (Harrison 1963, Casagrande 1979, DeVries 1987, Srygley 1994). Larvae generally consume large quantities of plant material to reach maturity, a behavior that may be related as much to the low nutrient content of their larval food plants (Auerbach & Strong 1981) as to their large body size (e.g., 15 g for a living, mature larva of *Caligo memnon* (Felder), DeVries 1983). Several species of brassolines lay eggs in clusters, and their larval feeding activity may produce remarkable damage to their food plants. For example, two *Caligo memnon* females were reported to lay, jointly, 165 eggs on banana plants in approximately three weeks in an outdoor enclosure (Young & Muyschondt 1985). *Caligo* caterpillars were reported to cause severe damage to banana plantations (Malo & Willis 1961, Harrison 1962, 1963, 1964), and larvae of *Brassolis isthmia* Bates are known to defoliate coconut palms (Dunn 1917; R. B. Srygley, C. M. Penz pers. obs.).

Apart from studies of population control (Malo & Willis 1961, Harrison 1962, 1964), few investigations have focused on the early stage biology of *Caligo* (see Young & Muyschondt 1985, and references therein). Here we describe the complete life cycle of *C. illioneus oberon* Butler, describe a mature larva of *C. idomeneus* (L.), and review larval food plant records for 39 brassoline species.

METHODS

Between 25 May and 31 December, 1994 we searched for ovipositing female butterflies along Pipeline Road, Soberania National Park, Panama, motivated by a study on *Caligo* mating behavior (Srygley & Penz 1999). The study area was a mosaic of old secondary and primary forests and pasture grasses with approximately 2.2 m annual precipitation (Ridgely 1976) and a wet season extending from late April to mid December. Our observations showed that *C. illioneus oberon* oviposit mostly at dusk (approx. 1700–1900 h) and only occasionally at dawn (0530–0630 h), and we therefore concentrated our observations in the twilight hours. Field collected early stages were reared in plastic containers at ambient temperature (25–29°C).

Wild female *Caligo illioneus oberon* were captured in two traps at the edge of the forest along Pipeline Road. To induce oviposition, captured females were released into an outdoor insectary (3 × 3 × 3 m) inside of which grew *Musa sapientum* L. and *Heliconia latispatha* Benth. (Musaceae), *Calathea latifolia* (Link) K. (Marantaceae), and three species of unidentified palms (Arecaceae). Females were supplied also with fresh cut leaves of *Saccharum spontaneum* L. (Poaceae) and *Cyrtostachys* sp. (Arecaceae), both exotics on which we had observed oviposition by female *Caligo illioneus* and *Opsiphanes* sp. respectively (R. B. Srygley pers. obs.).

Preserved larvae and pupal skins of *C. illioneus oberon* are in the collection of the Milwaukee Public Museum. The head capsule and pupal skin of *C. idomeneus* are currently in the Smithsonian Tropical Research Institute, to be relocated to the National Museum of Natural History in the future.

## RESULTS

### *Caligo illioneus oberon* Butler

**Oviposition behavior and food plants.** In the field, females laid clusters of 9–13 eggs ( $n = 4$  clusters) in a row along the midvein on the underside of medium-aged to old leaf blades of *Saccharum spontaneum*, an introduced Asian grass that invaded natural grasslands of Panama during the 1970's. Following its introduction, *S. spontaneum* gradually replaced the pasture grasses *Hyparrhenia rufa* (Nees) Stapf and *Panicum maximum* Jacq. (both introduced from Africa) on Pipeline Road (N. Smith pers. comm.). The native larval food plant for *C. illioneus* is not known in Panama, and our captive females did not oviposit on any of the plants available in the insectary.

**Egg** (developmental time = 6 days,  $n = 13$ ). White, spherical, approximately 1.5 mm wide, adorned with vertical ribs; description refers to a cluster of 13 eggs laid 27 August 1994.

**First instar** (duration = 8 days,  $n = 4$ ). **Head:** brown with simple black setae; two dark brown vertical stripes flank epicranial and frontal sutures from apex of head, terminating at approximately halfway the length of the front. **Body:** translucent green; broad, lemon-yellow middorsal stripe bordered by an irregular reddish-brown stripe that is prominent on the thorax and divided by a thin white discontinuous midline stripe that is more prominent on the thorax than on the abdomen; two thin, lateral, lemon-yellow longitudinal stripes; thoracic and abdominal legs grayish-white; ventral side grayish-white; caudae held separated, reddish to dark brown, each with a black sub-terminal seta arising at one-third to one-half the length of the caudae, and a terminal seta which is white at base and black at tip. The larvae molted synchronously.

**Second instar** (duration = 5 days,  $n = 4$ ). **Head:** dark brown anteriorly, lateral and post-genal regions translucent white; three pairs of scoli: dorsal scoli light brown (approximately half the height of the head), subdorsal scoli whitish (two-thirds the height of the dorsal scoli), lateral scoli whitish (approximately one-third the height of the subdorsal scoli); front dark brown; two thin whitish lines arise from base of dorsal scoli, converge toward and flank epicranial suture, ter-

minating at upper end of front; frontal suture whitish. **Body:** predominantly green; brown middorsal stripe divided by discontinuous white midline stripe; thoracic and abdominal legs grayish white; ventral side grayish white; caudae held separated, pink with black tips and numerous short white setae. The larvae molted synchronously.

**Third instar** (duration = 5–6 days,  $n = 4$ ). **Head:** as in second instar. **Body:** as in second instar, except for a broad, red lateral line divided by a thin, white spiracular stripe; single dark brown triangular middorsal projection at posterior end of abdominal segment A3. Shed caudae were not eaten after molt to fourth instar. Larvae molted asynchronously.

**Fourth instar** (duration = 6–7 days,  $n = 4$ ). **Head:** patterned in creamy-white and dark brown; dorsal scoli light brown anteriorly and reddish-brown posteriorly at the base (approximately same height as the head); subdorsal scoli creamy-white (approximately two-thirds the length of dorsal scoli); lateral scoli creamy-white (approximately one-half the length of the subdorsal scoli); one pair of creamy-white tubercles below lateral scoli; epicranial suture darkened; front creamy-white with vertical, medial brown stripe; two brown stripes arise from the base of dorsal scoli converge toward and flank epicranial and frontal sutures, terminating halfway down the length of the front; adfrontal region dark brown above stemmatal region; post-genae reddish-brown; base of head reddish-brown from occiput to mandibles; mandibles creamy-white, darkened at the cutting edge. **Body:** color varied from light mustard to greenish; thoracic segments T1 and T2 with middorsal white midline stripe, flanked by reddish stripes; remaining segments with thin grayish middorsal stripe; large reddish-brown, triangular middorsal projection located at posterior end of abdominal segment A3; very small middorsal projection at posterior end of A5; supra-spiracular white stripe along the entire length of the body; white sub-spiracular stripe on a continuous longitudinal swelling; thoracic and abdominal legs reddish; ventral side red; caudae pale pinkish-brown patterned with reddish-brown dorso-laterally, where pattern develops into thin broken lines. The larvae molted asynchronously and three out of four aggregated at rest.

**Fifth instar** (duration = 6–7 days,  $n = 4$ , Fig. 1a). **Head:** as in fourth instar, except for a brown stripe arising from dorsal scoli that flanks the epicranial and frontal sutures, and terminates above antennal socket; head densely covered with short creamy-white setae. **Body:** predominantly beige; dark brown middorsal stripe runs along entire length of body; on segments T1, T2, and anterior end of T3, the dark brown mid-



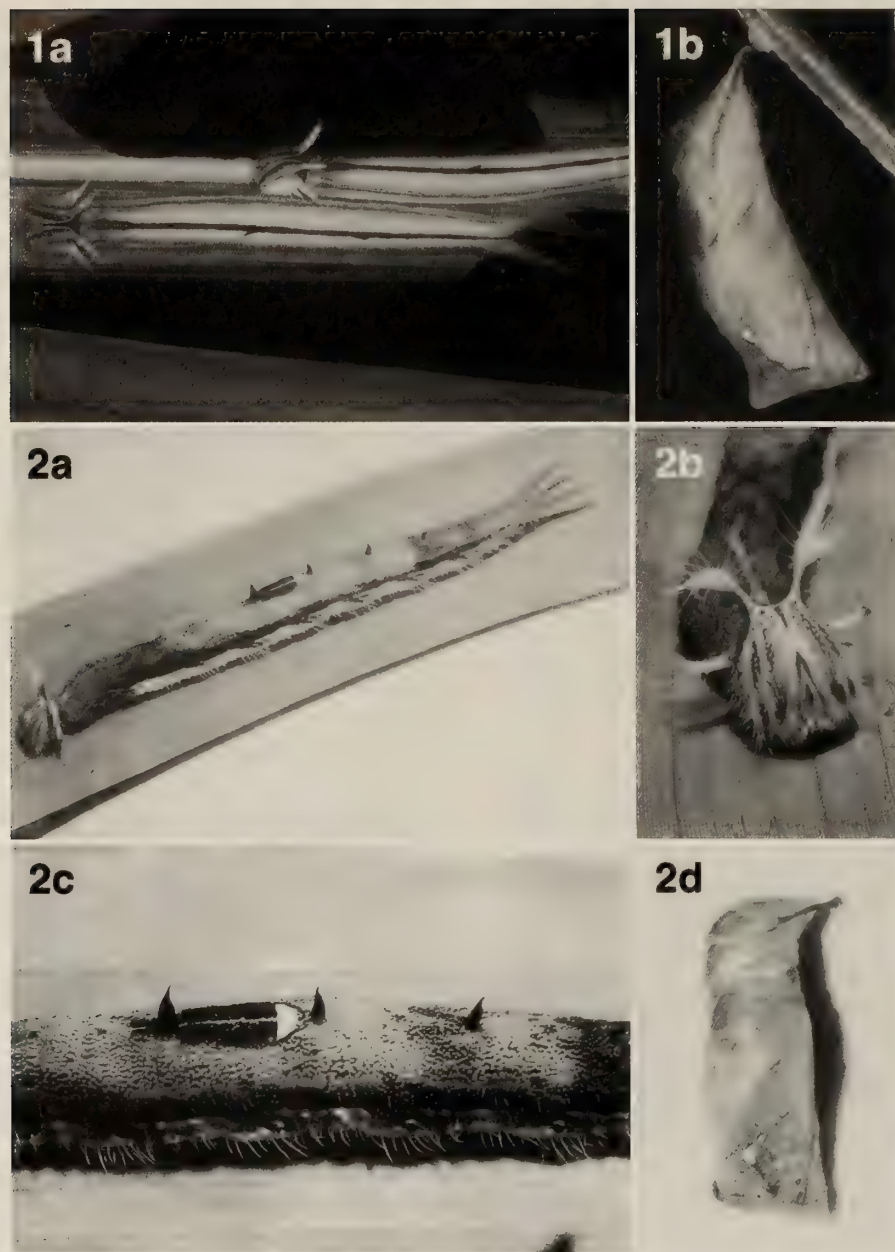


FIG. 1. *Caligo illioneus oregon*, photographs by R. Srygley; (a) fifth instar (October, 1994); (b) pupa (24 October, 1994). FIG. 2. *Caligo idomeneus* (Aiello Lot 81-77), photographs by A. Aiello; (a) final instar (2 December, 1981); (b) final instar, head (2 December, 1981); (c) final instar, body detail (2 December, 1981); (d) pupa (23 December, 1981).

dorsal stripe is divided by a thin creamy-white stripe; triangular middorsal projections same as in fourth instar; body patterned with brown from dorsal midline towards the sides, where pattern develops into thin, broken, longitudinal brown lines; dark brown supra-spiracular line bordered by creamy-white lines; creamy-white subspiracular stripe on a continuous longitudinal swelling; ventral side pink; caudae held separated, light brown at base, becoming dark brown at tip, approxi-

mately two-thirds the length of the head. Larvae molted asynchronously and did not aggregate at rest.

**Sixth instar** (duration = 14–16 days,  $n = 3$ ). **Head:** as in fifth instar, except for four pairs of scoli; additional stripe from dorsal scoli terminating above stem-matal region; dorsal scoli dark brown with white tips and basal creamy-white spots posteriorly; subdorsal and lateral scoli posteriorly brown at base; sub-lateral scoli dark brown posteriorly (one-half of the length of

the lateral scoli). **Body:** as in fifth instar, except for small dark brown triangular middorsal projection at posterior end of abdominal segment A2; large triangular middorsal projection at posterior end of A3; and small triangular middorsal projections at posterior ends of A4 and A5; ventral side brown; caudae held separated, slightly longer than head height.

**Larval development and behavior.** Egg development took 6 days ( $n = 13$ ) and larval development (from hatching to pupation) took 44–49 days ( $n = 3$ ). First through fourth instar larvae fed gregariously and generally rested together on the leaf blade. Fifth and sixth instar larvae rested away from each other on the stem of the plant. Late instar larvae found in the field were solitary (R. B. Srygley pers. obs.).

**Pupa** (duration = 13–15 days,  $n = 3$ , Fig. 1b). Beige with fine, dark brown cryptic markings, giving the general appearance of a dried, curled and sun-bleached leaf; head with transverse keel at apex; long, black setae located immediately above and on the surface of the eyes; antennae with a black longitudinal stripe, and a black transverse line marking each antennal segment; thoracic segment T2 with a prominent keel along dorsal midline, more developed in female than in male pupae; posterior edge of wing pad forming a crest; prominent hump at the base of wing pad; wing surface with two small silver spots located near base of wing; abdomen with conspicuous long black setae along dorsal midline; abdominal segments A5–10 with dark brown lateral line, A4–10 with brown ventral line; A6 humped; brown middorsal stripe arising at head and terminating at cremaster; abdominal segments with transverse oblique markings that resemble leaf venation. Pupal mass: 2.3 g ( $n = 1$ , male).

### *Caligo idomeneus* (L.)

A wandering final instar larva of *C. idomeneus* was found off the food plant by R. Kimsey at Fort Clayton (Canal Area, Panama) on 1 December, 1981 and reared to adult (Aiello Lot 81-77). The larva had about 15 white fly eggs cemented to the underside of the thorax and head. The eggs were removed with forceps and preserved in 80% ethanol. The oviposition behavior and larval food plants of *C. idomeneus* are unknown, but the captive mature larva readily accepted *Heliconia latispatha* Benth. (Musaceae) and *Calathea latifolia* (Link.) K. (Marantaceae) which it ate for 20 days prior to pupation.

**Final instar** ( $n = 1$ , Figs. 2a–c). **Head:** beige with brown stripes; three pairs of beige scoli: largest scoli dorsal, clothed in long setae, enlarged towards the pointed apex and abruptly curved outward toward the sides of the head; subdorsal scoli about two thirds the

length of the dorsal scoli, clothed in long setae, gently curved upwards to pointed apex; lateral scoli smallest, about one half the length of the subdorsals, conical; front with dark vertical dash; adfrontal area dark brown; upper section of epicranial suture dark brown; broad stripe lateral to adfrontal area, terminating at stemmatal level with a darker vertical dash; broad stripe from base of dorsal scoli, terminating on stemmata with a darker vertical dash; dark brown stripe from mid point of inside of each dorsal scoli, terminating at epicranial suture; dark brown stripe along curve from mid point of outside of each dorsal scoli, to sides of head just in front of subdorsal scoli; base of head dark brown from occiput to mandibles. **Body:** brown, except paler dorsally on abdominal segments A2–A6; broad subspiracular white stripe on A1–A7 with oblique brown intrusions from above, just posterior to each spiracle on A2–A7; four soft laterally flattened triangular middorsal projections, one on each of A3–A6; large oval middorsal spot, lying between the projections of A3 and A4, dark brown with a beige posterior-pointing arrow; caudae held separated, brown, broad.

**Pupa** (17 days, Fig. 2d). About 4.5 cm long, and 2 cm wide at widest point; beige with fine brown cryptic markings, giving the general appearance of a dried, curled and sun-bleached leaf; head ridged from center of eye to vertex; eye area adorned with stout dark brown upright setae; antennae with a median black stripe for their entire length, and with cross lines set approximately 0.5 mm apart; mesothorax mid-dorsally humped and keeled; a lateral keel begins near the thoracic spiracle, passes along the forewing, parallel to the inner margin, and, at a level with abdominal segment A1, smooths to become a raised area following the forewing inner margin to the tornus; each forewing bears two white enameled triangles toward the base of the inner margin and just ventral to the wing keel; clear patches and a small dark triangle are found at the midpoint of each mesothoracic leg; on the abdomen a dark brown midventral line terminates at the tip of the cremaster, as does an oblique dark brown line that begins at the spiracle on abdominal segment A6; dorsum adorned with dark brown, upright setae from the mesothoracic hump through abdominal segment A8, on which the setae are somewhat appressed; spiracles narrowly elliptical, and that of A8 is obscure.

**Diagnostic characters of early stage morphology.** The mature larvae of Central American species of *Caligo* can be easily diagnosed by head and body color, and by the number and morphology of the head scoli. The mature larva of *Caligo eurilochus sulanus* Fruhstorfer has a dark tan head adorned with four pairs of



TABLE 1. Larval food plants of the butterfly subfamily Brassolini (Nymphalidae). Abbreviations: ARE = Arecales, BRO = Bromeliales, CYC = Cyclanthaceae, GEN = Gentianales, gym = gymnosperm, POA = Poales, ZIN = Zingiberales, ovip = oviposition record. References: Aiello, unpubl<sup>1</sup>; Aiello & Silberglied, 1978<sup>2</sup>; Barcant, 1970<sup>3</sup>; Biezanko et al., 1974<sup>4</sup>; Burmeister, 1873<sup>5</sup>; Casagrande, 1979<sup>6</sup>; Condie, 1976<sup>7</sup>; Cubero, 1985<sup>8</sup>; d'Almeida, 1922<sup>9</sup>; d'Araújo e Silva et al., 1968<sup>10</sup>; DeVries, 1985<sup>11</sup>, 1987<sup>12</sup>; Fontaine, 1913<sup>13</sup>; Harrison, 1963<sup>14</sup>; Hayward, 1969<sup>15</sup>; Moss, unpubl (in Ackery, 1988)<sup>16</sup>; Müller, 1886<sup>17</sup>; Rothschild, 1916<sup>18</sup>; Small, unpubl<sup>19</sup>; Srygley, unpubl<sup>20</sup>; Srygley & Penz, unpubl<sup>21</sup>; Stauffer et al., 1993<sup>22</sup>; Ulrich & Boos, 1981<sup>23</sup>; Ulrich & Emmel, 1991<sup>24</sup>; Yepez et al., 1985<sup>25</sup>; Young, 1977<sup>26</sup>, 1986<sup>27</sup>; Young & Muyschondt, 1975<sup>28</sup>, 1985<sup>29</sup>.

Butterfly species	Plant order	family	species	Reference
1. <i>Blepolenis</i> (as <i>Opsiphanes</i> ) <i>batea</i> (Hübner)	ARE	Arecaceae	"palm"	18
	POA	Poaceae	<i>Panicum lanatum</i> Sw. (as capim amargoso)	10 (no. 2388)
<i>Blepolenis batea</i> (Hübner)	ARE	Arecaceae	<i>Arecastrum</i> (as <i>Syagrus</i> ) <i>romanzoffianum</i> (Cham.) Becc.	4
	ARE	Arecaceae	<i>Butia</i> (as <i>Syagrus</i> ) <i>capitata</i> (Mart.) Becc.	4
2. <i>Brassolis astyra</i> Godart	ARE	Arecaceae	"diversas especies de Palmae"	15
	ARE	Arecaceae	"palmen"	17
<i>Brassolis astyra astyra</i> Godart	ARE	Arecaceae	<i>Arecastrum</i> (as <i>Cocos</i> ) <i>romanzoffianum</i> (Cham.) Becc. (as gerivá)	10 (no. 2362)
	ARE	Arecaceae	<i>Astrocaryum ayri</i> Mart. (as brejauva)	10 (no. 2362)
	ARE	Arecaceae	<i>Bactris</i> sp.	10 (no. 2362)
	ARE	Arecaceae	<i>Butia</i> (as <i>Cocos</i> ) <i>eriospatha</i> (C. Mart. ex Drude) Becc. (as butiázeiro)	10 (no. 2362)
	ARE	Arecaceae	<i>Cocos nucifera</i> L. (as baba de boi)	10 (no. 2362)
	ARE	Arecaceae	<i>Cocos nucifera</i> L. (as coqueiro da Bahia)	10 (no. 2362)
	ARE	Arecaceae	<i>Cocos nucifera</i> L. (as coqueiro anão)	10 (no. 2362)
	ARE	Arecaceae	<i>Copernicia cerifera</i> Mart. (as carnaubeira)	10 (no. 2362)
	ARE	Arecaceae	<i>Livistona chinensis</i> (Jacq.) R. Br. (as pent-são da China)	10 (no. 2362)
	ARE	Arecaceae	<i>Livistona rotundifolia</i> (Lamarck) Mart.	10 (no. 2362)
	ARE	Arecaceae	<i>Phoenix dactylifera</i> L. (as tamareira)	10 (no. 2362)
	ARE	Arecaceae	<i>Roystonea</i> (as <i>Oreodoxa</i> ) <i>oleracea</i> (Jacq.) O.F. Cook (as palmeira imperial)	10 (no. 2362)
	ARE	Arecaceae	<i>Roystonea</i> (as <i>Oreodoxa</i> ) <i>regia</i> (Kunth) O.F. Cook (as palmeira real)	10 (no. 2362)
	POA	Poaceae	<i>Saccharum officinarum</i> L. (as cana de açúcar)	10 (no. 2362)
	ZIN	Musaceae	<i>Musa sapientum</i> L. (as bananeira)	10 (no. 2362)
3. <i>Brassolis isthmia</i> Bates	ARE	Arecaceae	<i>Chaemodora</i> sp.	27
	ARE	Arecaceae	<i>Cocos nucifera</i> L.	12
4. <i>Brassolis sophorae</i> (L.)	ARE	Arecaceae	<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.	22
	ARE	Arecaceae	<i>Archontophoenix alexandrae</i> (Muell.) H. Wendl. & Drude	22
	ARE	Arecaceae	<i>Arecastrum romanzoffianum</i> (Cham.) Becc.	22
	ARE	Arecaceae	<i>Astrocaryum</i> spp.	10 (no. 2365)
	ARE	Arecaceae	<i>Attalea</i> sp.	10 (no. 2365)
	ARE	Arecaceae	<i>Bactris major</i> Jacq.	22
	ARE	Arecaceae	<i>Bactris</i> spp.	10 (no. 2365)
	ARE	Arecaceae	<i>Butia</i> (as <i>Cocos</i> ) <i>eriospatha</i> (C. Mart. ex Drude) Becc. (as butiázeiro)	10 (no. 2365)
	ARE	Arecaceae	<i>Caryota mitis</i> Lour. (as <i>C. plumosa</i> horticola)	22
	ARE	Arecaceae	<i>Caryota urens</i> L.	22
	ARE	Arecaceae	<i>Chrysalidocarpus lutescens</i> H. Wendl.	22
	ARE	Arecaceae	<i>Chrysalidocarpus lutescens</i> H. Wendl. (as areca bambú)	10 (no. 2364)
	ARE	Arecaceae	<i>Cocos nucifera</i> L.	3, 15, 22
	ARE	Arecaceae	<i>Cocos nucifera</i> L. (as coqueiro da Bahia)	10 (nos 2363–2365)
	ARE	Arecaceae	<i>Cocos nucifera</i> L. (as coqueiro anão)	10 (no. 2365)
	ARE	Arecaceae	<i>Copernicia cerifera</i> Mart. (as carnaúba)	10 (no. 2365)
	ARE	Arecaceae	<i>Desmoncus</i> spp.	10 (no. 2365)
	ARE	Arecaceae	<i>Euterpe</i> spp.	10 (no. 2365)
	ARE	Arecaceae	<i>Hyophorbe lagenicaulis</i> (L.H. Bailey) H.E. Moore	22
	ARE	Arecaceae	<i>Livistona chinensis</i> (Jacq.) R. Br. (as pent-são da China)	10 (nos 2364, 2365)
	ARE	Arecaceae	<i>Livistona</i> sp.	22
	ARE	Arecaceae	<i>Mauritia flexuosa</i> L. f.	22
	ARE	Arecaceae	<i>Neodypsis decaryi</i> Jumelle	22
	ARE	Arecaceae	<i>Orbignya</i> spp.	10 (no. 2365)
	ARE	Arecaceae	"palms"	18
	ARE	Arecaceae	<i>Phoenix canariensis</i> hort. ex Chabaud	22
	ARE	Arecaceae	<i>Phoenix dactylifera</i> L.	22
	ARE	Arecaceae	<i>Phoenix dactylifera</i> L. (as tamareira)	10 (no. 2365)

TABLE 1. Continued.

Butterfly species	Plant: order	family	species	Reference
	ARE	Arecaceae	<i>Phoenix reclinata</i> Jacq.	22
	ARE	Arecaceae	<i>Pritchardia pacifica</i> Seemann and Wendland	22
	ARE	Arecaceae	<i>Ptychosperma macarthurii</i> (A.A. Wendl.) G. Nicholson	22
	ARE	Arecaceae	<i>Roystonea</i> (as <i>Oreodoxa</i> ) <i>oleracea</i> (Jacq.) O.F. Cook (as palmeira imperial)	10 (nos 2364, 2365)
	ARE	Arecaceae	<i>Roystonea</i> (as <i>Oreodoxa</i> ) <i>regia</i> (Kunth) O.F. Cook (as palmeira real)	10 (nos 2364, 2365)
	ARE	Arecaceae	<i>Roystonea oleracea</i> (Jacq.) O.F. Cook	25
	ARE	Arecaceae	<i>Roystonea regia</i> (Kunth) O.F. Cook	22
	ARE	Arecaceae	<i>Roystonea venezuelana</i> L.H. Bailey	22
	ARE	Arecaceae	<i>Sabal mauritiformis</i> (H. Karst.) Griseb. and H. Wendl.	22
	ARE	Arecaceae	<i>Sabal umbraculiferus</i> Mart.	22
	ARE	Arecaceae	<i>Scheelea macrocarpa</i> Karsten	22
	ARE	Arecaceae	<i>Washingtonia filifera</i> (Linden ex André) H. Wendl.	22
	POA	Poaceae	<i>Saccharum officinarum</i> L. (as cana de açúcar)	10 (no. 2365)
	ZIN	Musaceae	<i>Musa sapientum</i> L. (as bananeira)	10 (no. 2365)
	ZIN	Musaceae	<i>Ravenala madagascariensis</i> Sonn.	22
	ZIN	Musaceae	<i>Strelitzia nicolai</i> Regel & Körn.	22
5. <i>Caligo arisbe</i> Hübner	ZIN	Marantaceae	Caetê	10 (no. 2369)
6. <i>Caligo atreus</i> Kollar	ARE	Arecaceae	<i>Asterogyne martiana</i> H. Wendl. (H. Wendl.) ex Hemsl.	11
	ZIN	Marantaceae	<i>Calathea</i> sp.	7
	ZIN	Musaceae	<i>Heliconia</i> spp.	11, 29
<i>Caligo atreus dionysos</i> Fruhstorfer	CYC	Cyclanthaceae	Cyclanthus	12
	ZIN	Musaceae	<i>Heliconia</i> sp.	12
	ZIN	Musaceae	<i>Musa</i> sp.	12
7. <i>Caligo beltrao</i> (Illiger)	ZIN	Cannaceae	<i>Canna indica</i> L.	6
	ZIN	Marantaceae	Caetê	10 (no. 2367)
	ZIN	Marantaceae	<i>Calathea zebrina</i> (Sims) Lindl.	6
	ZIN	Musaceae	<i>Musa sapientum</i> L. (as bananeira)	10 (no. 2367)
	ZIN	Musaceae	"plusieurs <i>Musaceae</i> "	9
	ZIN	Zingiberaceae	<i>Hedychium coronarium</i> J. König (as lírio do brejo)	10 (no. 2367)
8. <i>Caligo eurilochus</i> (Cramer)	ZIN	Marantaceae	<i>Calathea latifolia</i> (Willd. ex Link.) Klotzsch	20
	ZIN	Musaceae	<i>Hedychium</i> sp.	17
	ZIN	Musaceae	<i>Heliconia latispatha</i> Benth.	1 (lot 80-26)
	ZIN	Musaceae	<i>Heliconia latispatha</i> Benth.	20 (ovp)
	ZIN	Musaceae	<i>Musa sapientum</i> L.	20 (ovp)
	ZIN	Musaceae	"plusieurs <i>Musaceae</i> (sic)"	9
<i>Caligo eurilochus brasiliensis</i> (Felder)	ARE	Arecaceae	<i>Euterpe edulis</i> Mart. (as palmito)	10 (no. 2368)
	ZIN	Musaceae	banana	18
	ZIN	Musaceae	<i>Musa sapientum</i> L. (as bananeira)	10 (no. 2368)
<i>Caligo eurilochus sulanus</i> Fruhstorfer	ZIN	Zingiberaceae	<i>Hedychium coronarium</i> J. König (as lírio do brejo)	10 (no. 2368)
	ZIN	Marantaceae	<i>Calathea</i> sp.	12
	ZIN	Musaceae	<i>Heliconia</i> sp.	12
	ZIN	Musaceae	<i>Musa</i> sp.	12
9. <i>Caligo idomeneus</i> (L.)	ZIN	Marantaceae	unidentified	15
	ZIN	Musaceae	<i>Heliconia latispatha</i> Benth.	1 (lot 81-77)
	ZIN	Musaceae	<i>Musa</i> sp.	16
10. <i>Caligo illioneus</i> (Cramer)	ZIN	Marantaceae	<i>Hedychium coronarium</i> J. König (as lírio do brejo)	10 (no. 2371)
	ZIN	Musaceae	<i>Heliconia</i> spp.	11
	ZIN	Musaceae	<i>Musa sapientum</i> L. (as bananeira)	10 (no. 2371)
<i>Caligo illioneus oberon</i> Butler	POA	Poaceae	<i>Saccharum spontaneum</i> L.	21
	ZIN	Musaceae	<i>Heliconia</i> sp.	12
	ZIN	Musaceae	<i>Musa</i> sp.	12
<i>Caligo illioneus pampeiro</i> Fruhstorfer	ZIN	Musaceae	banana	18
11. <i>Caligo martia</i> (Godart)	POA	Poaceae	<i>Echinochloa crus-galli</i> (L.) P. Beauv. (as capim canivão)	10 (no. 2372)
	POA	Poaceae	<i>Pennisetum purpureum</i> Schumach. (as capim elefante)	10 (no. 2372)
12. <i>Caligo memnon</i> (Felder & Felder)	ZIN	Cannaceae	<i>Canna indica</i> L.	1 (lot 85-57)
	ZIN	Cannaceae	<i>Canna</i> sp.	7
	ZIN	Marantaceae	<i>Calathea latifolia</i> (Willd. ex Link.) Klotzsch	20 (ovp)
	ZIN	Musaceae	<i>Heliconia latispatha</i> Benth.	20, 29
	ZIN	Musaceae	<i>Heliconia</i> spp.	7, 11, 19
	ZIN	Musaceae	<i>Musa sapientum</i> L.	20 (ovp)
	ZIN	Musaceae	<i>Musa</i> sp.	14, 29



TABLE 1. Continued.

Butterfly species	Plant: order	family	species	Reference
<i>Caligo memnon memnon</i> (Felder & Felder)	ZIN	Musaceae	<i>Heliconia</i> sp.	12
	ZIN	Musaceae	<i>Musa</i> sp.	12
<i>Caligo memnon telamonius</i> (Felder & Felder)	GEN	Rubiaceae	<i>Coffea</i> sp. (as cafeeiro) [dubious record]	10 (no. 2373)
13. <i>Caligo oberthurii oberthurii</i> (Deyrolle)	ARE	Arecaceae	"low, evergreen palm"	18
14. <i>Caligo oileus</i> (Felder & Felder)	ZIN	Musaceae	<i>Musa</i> sp.	16
<i>Caligo oileus scamander</i> (Boisduval)	ZIN	Musaceae	<i>Heliconia</i> sp.	12
15. <i>Caligo placidianus</i> Staudinger	ZIN	Musaceae	<i>Musa</i> sp.	16
16. <i>Caligo praxsiodus</i> Fruhstorfer	POA	Poaceae	<i>Saccharum officinarum</i> L. (as cana de açúcar)	10 (no. 2374)
17. <i>Caligo prometheus epimetheus</i> (Felder & Felder)	ZIN	Musaceae	banana	18
18. <i>Caligo teucer</i> (L.)	ZIN	Musaceae	<i>Heliconia</i> sp.	16
	ZIN	Musaceae	<i>Musa</i> sp.	3
<i>Caligo</i> sp.	ARE	Arecaceae	<i>Cyrtostachys</i> sp.	20
	ZIN	Musaceae	<i>Musa sapientum</i> L. (as bananeira)	10 (no. 2366)
	ZIN	Zingiberaceae	<i>Hedychium coronarium</i> J. König (as lírio do brejo)	10 (no. 2366)
19. <i>Catoblepia amphirhoe</i> (Hübner)	ARE	Arecaceae	<i>Arecastrum</i> (as <i>Cocos</i> ) <i>romanzoffianum</i> (Cham.) Becc. (as gerivá)	10 (no. 2375)
	ARE	Arecaceae	"palmeras"	15
20. <i>Catoblepia orgetorix championi</i> Bristow	ARE	Arecaceae	palms	12
21. <i>Dasyophthalma rusina</i> (as <i>geraensis</i> ) (Godart)	ARE	Arecaceae	<i>Bactris tomentosa</i> Mart. (as uricana)	10 (no. 2376)
<i>Dasyophthalma rusina</i> (Godart)	ARE	Arecaceae	<i>Euterpe edulis</i> Mart. (as palmito)	10 (no. 2377)
	POA	Poaceae	<i>Bambusa</i> sp. (as bambú)	10 (no. 2378)
22. <i>Dynastor darius</i> (F.)	BRO	Bromeliaceae	<i>Aechmea fasciata</i> (Lindl.) Baker	10 (no. 2381)
	BRO	Bromeliaceae	<i>Aechmea nudicaulis</i> (L.) Griseb.	24
	BRO	Bromeliaceae	<i>Ananas comosus</i> (as <i>sativus</i> ) (L.) Merr. (as abacaxi)	10 (nos 2379–2381)
	BRO	Bromeliaceae	<i>Ananas</i> sp. (as ananás selvagem)	10 (no. 2379)
	BRO	Bromeliaceae	<i>Ananas</i> sp. (as ananás)	10 (no. 2379)
	BRO	Bromeliaceae	<i>Billbergia nutans</i> H. Wendl. ex Regel	10 (no. 2381)
	BRO	Bromeliaceae	<i>Billbergia speciosa</i> Thunb.	10 (no. 2381)
	BRO	Bromeliaceae	<i>Billbergia</i> spp.	10 (no. 2380)
	BRO	Bromeliaceae	<i>Bromelia fastuosa</i> Lindl. (as bananilha do mato)	10 (no. 2381)
	BRO	Bromeliaceae	<i>Bromelia fastuosa</i> Lindl. (as caraguatá)	10 (nos 2379, 2380)
	BRO	Bromeliaceae	<i>Bromelia fastuosa</i> Lindl. (as banana do mato)	10 (no. 2379)
	BRO	Bromeliaceae	<i>Ortgiesia</i> (as <i>Aechmea</i> ) <i>gamosepala</i> (Wittm.) L.B. Sm. & W.J. Kress	10 (no. 2381)
	BRO	Bromeliaceae	<i>Tillandsia zebrina</i> hort. ex Baker	10 (no. 2379)
	BRO	Bromeliaceae	unidentified	17
<i>Dynastor darius mardonius</i> Fruhstorfer	BRO	Bromeliaceae	unidentified	15
<i>Dynastor darius stygianus</i> Butler	BRO	Bromeliaceae	<i>Aechmea magdalenae</i> (André) André ex Baker	11
	BRO	Bromeliaceae	<i>Aechmea</i> sp.	12
	BRO	Bromeliaceae	<i>Agallostachys pinguin</i> (L.) Beer (as <i>Bromelia pinguin</i> L.)	11
	BRO	Bromeliaceae	<i>Ananas comosus</i> (L.) Merr. [accepted by larvae in captivity]	2, 1 (lot 78-84)
	BRO	Bromeliaceae	<i>Ananas</i> sp.	12
	BRO	Bromeliaceae	<i>Bromelia plumieri</i> (E. Morren) L.B. Sm.	1
	BRO	Bromeliaceae	<i>Bromelia</i> sp.	12
	BRO	Bromeliaceae	"pineapple and other bromeliads, gravata"	18
23. <i>Dynastor macrosiris</i> (Doubleday)	BRO	Bromeliaceae	<i>Aechmea nudicaulis</i> (L.) Griseb.	23, 24
24. <i>Dynastor napoleon</i> (Doubleday)	BRO	Bromeliaceae	<i>Aechmea nudicaulis</i> (L.) Griseb.	24
	BRO	Bromeliaceae	<i>Aechmea</i> sp.	10 (no. 2382)
	BRO	Bromeliaceae	<i>Ananas comosus</i> (as <i>sativus</i> ) (L.) Merr. (as abacaxi)	10 (no. 2382)
	BRO	Bromeliaceae	gravata	18
25. <i>Eryphanis aesacus bubocula</i> (Butler)	ARE	Arecaceae	palms	12
	POA	Poaceae	<i>Bambusa vulgaris</i> Schrad. ex J.C. Wendl.	8
	POA	Poaceae	<i>Chusquea scabra</i> Soderstr. & C.E. Calderón	8
	POA	Poaceae	<i>Olyra caudata</i> Trin.	8
26. <i>Eryphanis automedon</i> (Cramer)	POA	Poaceae	<i>Bambusa</i> sp.	3
27. <i>Eryphanis polypena lycomedon</i> (Felder & Felder)	POA	Poaceae	bamboo	12
	POA	Poaceae	<i>Bambusa arundinacea</i> (Retz.) Willd.	1 (lot 82-9)
	POA	Poaceae	<i>Saccharum spontaneum</i> L.	1, 21
28. <i>Eryphanis reevesii</i> (Doubleday)	POA	Poaceae	<i>Bambusa</i> (as <i>Guadua</i> ) sp.	10 (no. 2383)
	POA	Poaceae	<i>Bambusa vulgaris</i> Schrad. ex J.C. Wendl. (as bambú comum)	10 (no. 2383)

TABLE 1. Continued.

Butterfly species	Plant: order	family	species	Reference
	POA	Poaceae	<i>Bambusa vulgaris</i> Schrad. ex J.C. Wendl. (as bambú comum)	10 (no. 2383)
	POA	Poaceae	<i>Olyra latifolia</i> L. (as taquarinha)	10 (no. 2383)
	POA	Poaceae	<i>Pennisetum purpureum</i> Schumach. (as capim elefante)	10 (no. 2383)
<i>Eryphanis reevesii</i> (Doubleday) (as <i>Caligo rivestii</i> )	POA	Poaceae	<i>Bambusa</i> sp.	17
	POA	Poaceae	<i>Olyra latifolia</i> L.	17
29. <i>Narope cyllastros</i> Doubleday	POA	Poaceae	<i>Bambusa</i> spp.	15, 17
<i>Narope cyllastros cyllastros</i> Doubleday	POA	Poaceae	<i>Bambusa</i> (as <i>Guadua</i> ) sp.	10 (no. 2384)
	POA	Poaceae	<i>Bambusa</i> sp. (as bambú)	10 (no. 2384)
<i>Narope cyllastros testacea</i> Godman & Salvin	POA	Poaceae	<i>Bambusa</i> sp.	12
30. <i>Opoptera aorsa</i> (Godart) (as <i>Opsiphanes aorosa</i> )	POA	Poaceae	<i>Bambusa vulgaris</i> Schrad. ex J.C. Wendl. (as bambú comum)	10 (no. 2387)
31. <i>Opoptera staudingeri</i> (Godman & Salvin)	POA	Poaceae	<i>Chusquea longifolia</i> Swallen	8
	POA	Poaceae	<i>Chusquea</i> sp.	12
<i>Opoptera</i> (as <i>Opsiphanes</i> ) <i>staudingeri</i> (Godman & Salvin)	POA	Poaceae	<i>Chusquea</i> sp.	11
32. <i>Opoptera</i> (as <i>Opsiphanes</i> ) <i>syme</i> (Hübner)	POA	Poaceae	<i>Bambusa</i> (as <i>Guadua</i> ) sp.	10 (no. 2395)
33. <i>Opsiphanes bogotanus</i> Distant	ARE	Arecaceae	palm	11, 12
	ZIN	Marantaceae	<i>Calathea inocephala</i> (Kuntze) H.A. Kenn. & Nicolson	1 (lot 81-41)
	ZIN	Marantaceae	<i>Calathea latifolia</i> (Willd. ex Link.) Klotzsch	20
<i>Opsiphanes bogotanus bogotanus</i> Distant	ZIN	Musaceae	banana	18
34. <i>Opsiphanes cassiae</i> (L.)	ARE	Arecaceae	unidentified	13
	ZIN	Musaceae	<i>Heliconia</i> sp.	16
	ZIN	Musaceae	<i>Heliconia</i> sp. and "différentes plantes musacées"	5
	ZIN	Musaceae	<i>Musa sapientum</i> L.	15
<i>Opsiphanes cassiae cassiculus</i> Stichel	ZIN	Musaceae	<i>Musa</i> sp.	3
<i>Opsiphanes cassiae lucullus</i> Fruhstorfer	ZIN	Musaceae	banana	18
	ZIN	Musaceae	<i>Musa sapientum</i> L. (as bananeira)	10 (no. 2389)
35. <i>Opsiphanes cassina aiellae</i> Bristow	ARE	Arecaceae	<i>Cocos nucifera</i> L.	1 (lots 77-76, 82-1, 83-17, 87-3)
	ARE	Arecaceae	<i>Livistona</i> sp.	1 (lot 91-25)
	ARE	Arecaceae	palm	1 (lot 95-8)
<i>Opsiphanes cassina fabricii</i> (Boisduval)	ARE	Arecaceae	<i>Acrocomia vinifera</i> Oerst.	11, 12
	ARE	Arecaceae	<i>Bactris guineensis</i> (L.) H.E. Moore (as <i>Bactris minor</i> )	28
	ARE	Arecaceae	<i>Bactris</i> sp.	11, 12
	ARE	Arecaceae	<i>Cocos nucifera</i> L.	11, 12, 28
	ARE	Arecaceae	<i>Erythea salvadorensis</i> (H.Wendl. ex Becc.) H.E. Moore (as <i>Brahea saldorensis</i> )	28
	ARE	Arecaceae	<i>Roystonea regia</i> (Kunth) O.F. Cook	28
36. <i>Opsiphanes invirae</i> (Hübner)	ARE	Arecaceae	<i>Arecastrum</i> (as <i>Cocos</i> ) <i>romanzoffianum</i> (Cham.) Becc. (as gerivá)	10 (nos 2390, 2392)
	ARE	Arecaceae	<i>Arecastrum</i> (as <i>Syagrus</i> ) <i>romanzoffianum</i> (Cham.) Becc.	4
	ARE	Arecaceae	<i>Butia</i> (as <i>Cocos</i> ) <i>eriospatha</i> (C. Mart. ex Drude) Becc. (as butiázeiro)	10 (nos 2390, 2392)
	ARE	Arecaceae	<i>Butia</i> (as <i>Syagrus</i> ) <i>capitata</i> (Mart.) Becc.	4
	ARE	Arecaceae	<i>Cocos nucifera</i> L. (as coqueiro da Bahia)	10 (no. 2390)
	ARE	Arecaceae	<i>Copernicia cerifera</i> Mart. (as carnaúba)	10 (no. 2390)
	ARE	Arecaceae	<i>Livistona australis</i> (R. Br.) C. Mart.	4
	ARE	Arecaceae	<i>Livistona australis</i> (R. Br.) C. Mart. (as pent-são austral)	10 (nos 2390, 2392)
	ARE	Arecaceae	<i>Livistona chinensis</i> (Jacq.) R. Br. (as pent-são chinês)	10 (no. 2392)
	ARE	Arecaceae	<i>Livistona chinensis</i> (Jacq.) R. Br.	4
	ARE	Arecaceae	<i>Livistona rotundifolia</i> (Lamarck) Mart.	10 (no. 2390)
	ARE	Arecaceae	Palmeira de leque	10 (no. 2392)
	ARE	Arecaceae	<i>Phoenix canariensis</i> hort. ex Chabaud	4
	ARE	Arecaceae	<i>Prestoea</i> sp.	8
	ARE	Arecaceae	<i>Raphia</i> sp. (as palmeira ornamental)	10 (no. 2391)
	ARE	Arecaceae	<i>Roystonea</i> (as <i>Oreodoxa</i> ) <i>oleracea</i> (Jacq.) O.F. Cook (as palmeira imperial)	10 (no. 2390)



TABLE 1. Continued.

Butterfly species	Plant: order	family	species	Reference
	gym	Cycadaceae	<i>Cycas circinalis</i> L. (as palmeira de jardim) [dubious record]	10 (no. 2390)
	ZIN	Musaceae	<i>Musa sapientum</i> L. (as bananeira)	10 (nos 2390, 2392)
<i>Opsiphanes invirae amplificatus</i> Stichel (as <i>O. i. remoliatius</i> )	ARE	Arecaceae	"giriva and palms"	18
<i>Opsiphanes invirae amplificatus</i> (Stichel)	ARE	Arecaceae	<i>Phoenix</i> sp.	15
<i>Opsiphanes invirae amplificatus</i> Stichel (as <i>ampliplacita</i> )	ZIN	Musaceae	<i>Musa sapientum</i> L. (as bananeira)	10 (no. 2386)
<i>Opsiphanes invirae cuspidatus</i> Stichel	ARE	Arecaceae	<i>Bactris major</i> Jacq.	1 (lot 82-44)
	ARE	Arecaceae	palms	12
37. <i>Opsiphanes merianae</i> Stichel	ARE	Arecaceae	ornamental palm	3
38. <i>Opsiphanes quiteria</i> (Cramer)	ARE	Arecaceae	<i>Arecastrum romanzoffianum</i> (Cham.) Becc.	15
<i>Opsiphanes quiteria badius</i> Stichel	ARE	Arecaceae	<i>Bactris</i> sp.	1 (lot 81-74)
<i>Opsiphanes quiteria meridionalis</i> Staudinger	ARE	Arecaceae	<i>Chrysalidocarpus</i> (as <i>Areca</i> ) <i>lutescens</i> H. Wendl.	10 (no. 2393)
<i>Opsiphanes quiteria meridionalis</i> (as <i>philon</i> ) Staudinger	ARE	Arecaceae	<i>Astrocaryum ayri</i> Mart. (as brejauva)	10 (no. 2394)
	ARE	Arecaceae	<i>Euterpe edulis</i> Mart. (as palmito)	10 (no. 2394)
<i>Opsiphanes quiteria quirinus</i> Godman & Salvin	ARE	Arecaceae	<i>Chrysalidocarpus lutescens</i> H. Wendl.	8
	ARE	Arecaceae	<i>Cocos nucifera</i> L.	26
	ARE	Arecaceae	<i>Geonoma</i> sp.	8
	ARE	Arecaceae	palms	12
	ARE	Arecaceae	<i>Prestoea allenii</i> H.E. Moore	8
39. <i>Opsiphanes tamarindi</i> Felder & Felder	ZIN	Musaceae	<i>Musa sapientum</i> L. (as bananeira)	10 (no. 2396)
	ZIN	Musaceae	<i>Musa</i> sp.	14, 17
<i>Opsiphanes tamarindi sikyon</i> Fruhstorfer	ZIN	Musaceae	<i>Heliconia collinsiana</i> Griggs	28
	ZIN	Musaceae	<i>Heliconia latispatha</i> Benth.	28
	ZIN	Musaceae	<i>Musa</i> sp.	28
<i>Opsiphanes tamarindi tamarindi</i> Felder & Felder	ZIN	Cannaceae	<i>Canna indica</i> L.	1 (lot 84-9)
	ZIN	Musaceae	<i>Heliconia latispatha</i> Benth.	1 (lots 80-40, 80-43)
	ZIN	Musaceae	<i>Heliconia</i> sp.	12
	ZIN	Musaceae	<i>Musa</i> sp.	12
<i>Opsiphanes</i> sp.	ARE	Arecaceae	<i>Cocos nucifera</i> L. (as coqueiro anão)	10 (no. 2385)
	ARE	Arecaceae	<i>Cyrtostachys</i> sp.	20
	ZIN	Musaceae	<i>Heliconia latispatha</i> Benth.	1 (lot 82-18)
	ZIN	Musaceae	<i>Musa sapientum</i> L. (as bananeira)	10 (no. 2385)

scoli, dark brown body with six middorsal projections (see figs. 6 and 7 in Malo & Willis 1961 p. 532). That of *C. atreus dionysos* Fruhstorfer has a tan colored head with fine vertical striations and three pairs of scoli,

with the dorsal pair enlarged at tip and curved outward (see fig. 32, E1 in DeVries 1987 p. 248), a tan colored body with many fine striations on dorsum, and five middorsal projections (DeVries 1987). The head cap-

TABLE 2. Summary of larval food plant records for brassoline butterflies. Numbers represent species as listed in Table 1.

Plant: order family	ARE Arecaceae	POA Poaceae	ZIN Musaceae	Marantaceae	Zingiberaceae	Canaceae	CYC Cyclanthaceae	BRO Bromeli- aceae
Butterfly genera								
<i>Blepipolis</i>	1							
<i>Brassolis</i>	2, 3, 4	2, 4	2, 4					
<i>Caligo</i>	6, 9, 14	11, 12, 17	6, 7, 8, 9, 10 12, 14, 15, 17, 18	5, 6, 7, 8, 9, 10, 12	7, 8	7, 12	6	
<i>Catoblepia</i>	19, 20							
<i>Dasyophthalma</i>	21	21						
<i>Dynastor</i>								22, 23, 24
<i>Eryphanis</i>	25	25, 26, 27, 28						
<i>Narope</i>		29						
<i>Opoptera</i>		30, 31, 32						
<i>Opsiphanes</i>	33, 34, 35, 36, 37, 38		33, 34, 36, 39	33		39		

sule of the mature larva of *C. memnon* is banded with tan and dark brown with four pairs of scoli (see fig. 5 in Young & Muysshondt 1985 p.162; fig. 32, E2 in DeVries 1987 p. 248), with the dorsal pair enlarged at tip. The body is light brown with a dark brown middorsal stripe, dark brown striations, and six middorsal projections (note that fig. 5 in Young & Muysshondt 1985 p.162, and fig. 31 F in DeVries 1987 p. 248, do not portray the same body color pattern). The mature larva of *C. illioneus* has a head patterned in brown and creamy white adorned with three pairs of scoli plus a lateral tubercle, and the body is beige with a dark brown middorsal stripe and four middorsal projections (Fig. 1a). That of *C. idomeneus* has a beige head patterned with brown, three pairs of scoli with the dorsal pair enlarged at tip and curved outward (Fig. 2b). The body is brown with a lighter colored area dorsally and a large oval middorsal spot between A3 and A4, a broad white subspiracular stripe, and four middorsal projections (Fig. 2a). The pupae of all species are very similar, and those of *C. illioneus* and *C. idomeneus* seem to differ only in the size of the white triangular marking at the base of the wing (more prominent in *C. idomeneus*, Fig. 2d). Early stages of *C. oileus* have never been formally described.

**Larval food plants of the Brassolinae.** It is well known that brassoline immatures are restricted to monocotyledonous plants (Ehrlich & Raven 1965, Ackery 1988, Table 1), but little correlation has been found between plant use and brassoline classification (Ackery 1988). We found that larval food plants include four of the eight monocot superorders (Table 1), a distribution suggesting that brassolines are generalist monocot feeders. However, all food plant records together indicate that the majority of species feed on plants in the families Arecaceae, Musaceae, and Poaceae (Tables 1 and 2). Therefore, the apparent lack of correspondence between plant use and brassoline classification should be reexamined.

Available records are sufficient to show that brassoline genera vary both in diet breadth and their association with monocot families (Table 2; see Stichel 1909 and Bristow 1981, 1982, 1991 for taxonomic classification of the butterflies). For instance, although individual species of *Caligo* have been reported to feed on 1–4 plant genera in 1–4 families, collectively *Caligo* has a larval food plant range that includes 11 genera in 7 families (Table 2, see also Ackery 1988) suggesting multiple events of host colonization during its evolutionary history. Similar patterns occur in *Eryphanes* and *Opsiphanes*: species of *Eryphanes* typically feed on Poaceae, except for *E. aesacus* which has also been found on Arecaceae; and *Opsiphanes* tend to associate

with Arecaceae and Musaceae, except for *O. bogotanus* and *O. tamarindi*, whose food plant range also includes Marantaceae and Canaceae respectively. Available information suggests that other brassolines are restricted to a single plant family (*Blepolenis* and *Catoblepia* on Arecaceae, *Narope* and *Opoptera* on Poaceae, *Dynastor* on Bromeliaceae). Noteworthy is that the food plant range of the putative basal genus *Brassolis* includes Arecaceae, Poaceae and Musaceae; the plant families upon which most brassolines feed as immatures. Although patterns of host association can be recognized at the generic level, their examination in an evolutionary context awaits a well supported phylogeny for this group of butterflies.

We hope that the summary presented here encourages research aimed at furthering our understanding of the patterns of food plant utilization and evolution in brassoline butterflies.

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## THE SPHINGIDAE (HETEROCERA) OF THE “EL OCOTE” RESERVE, CHIAPAS, MEXICO

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**ABSTRACT.** A study of the family Sphingidae was conducted in the Reserve, “El Ocote,” located in the northeast portion of the state of Chiapas, Mexico. Collections were made principally using a blacklight between 1994 and 1997. A total of 60 species were collected, from 20 genera in five tribes and three subfamilies. *Xylophanes*, *Manduca*, *Eumorpha* and *Erinnyis* had the greatest number of species. *Nyceryx mulleri* Clark is a new record for Chiapas. Eighty percent of the species were collected in the first two months of the rainy season. It was estimated that the present collection accounted for 75% of the species of Sphingidae in the reserve, based on the accumulation of species per collection effort. The fauna of the Sphingidae collected from “El Ocote” was compared with that reported from two other reserves of southern México, “Los Tuxtlas”, Veracruz and “Chajul”, Chiapas. “El Ocote” and “Chajul” were the most similar with 87% affinity.

**Additional key words:** tropical forests, biodiversity, neotropical region, invertebrate inventory.

**RESUMEN.** Se presenta un estudio faunístico de la familia Sphingidae de la selva “El Ocote”, ubicada al noreste del estado de Chiapas, México. Se efectuaron colectas con trampa de luz tipo pantalla entre 1994 y 1997, que aportaron 60 especies de 20 géneros comprendidos en cinco tribus y tres subfamilias. El mayor número de especies se distribuye en los géneros *Xylophanes*, *Manduca*, *Eumorpha* y *Erinnyis*. *Nyceryx mulleri* Clark es un nuevo registro para Chiapas. El 80% de las especies se colectó en los dos primeros meses de la temporada lluviosa. La estimación de la riqueza de especies por esfuerzo de colecta indica que esta investigación aporta el 75% de las especies de esta región. Se incluye una comparación con la fauna de Sphingidae de Los Tuxtlas, Veracruz y Chajul, Chiapas, resultando que El Ocote y Chajul presentan una afinidad de 87%.

There has been tremendous international publicity and concern surrounding the unprecedented rate at which tropical forests are being lost. The concern is well warranted because although tropical forests cover only about 7% of the terrestrial surface of the planet, they probably support around 50% of the flora and fauna (Myers 1986). Despite this diversity, these forests are increasingly threatened and destroyed.

Although much of the international attention has been directed at the larger tracts of tropical forest such as the Amazon and the Congo basin of Africa, Mexico has important tracts of tropical forests that merit serious conservation efforts. However, it is estimated that 80% of the tropical forests of Mexico have already been destroyed and those that remain are seriously threatened (Estrada et al. 1995). This is the case with the tropical forest reserve, “El Ocote” in the north-eastern Chiapas. Of the 48,140 hectares designated as reserve lands in 1982 (Diario Oficial de la Federación 1982), only 57%, (27,437 ha), can now be considered as forested and not directly affected by agricultural activities (García et al. 1996).

As for other tropical forests, a high diversity of vertebrates have been reported from “El Ocote” Reserve (Domínguez et al. 1996, Muñoz et al. 1996, Navarrete-Gutiérrez et al. 1996), but there is a lack of inventories of the invertebrate fauna. Knowledge of the invertebrate diversity could complement the findings con-

cerning the vertebrate fauna, and give further information on the species most threatened by habitat destruction, and, in general, give an indication of the biological significance of the reserve based on species richness (Toledo 1988).

The present study is a contribution to the knowledge of the Lepidoptera fauna of southeastern Mexico, and in particular, of the family Sphingidae of the “El Ocote” Reserve of northwestern Chiapas. An inventory was conducted of the Sphingidae of the Reserve, from which a comparison was made of the species richness of this family reported from two other tropical forests of southern Mexico. “Los Tuxtlas” of the Gulf Coast of Veracruz, and “Chajul” of the Lacandon region of eastern Chiapas. These forests, together with “El Ocote”, presumably formed a single tract of tropical forest stretching from the Gulf coast of Veracruz to what is now the border with Guatemala (Challenger 1998).

### MATERIALS AND METHODS

**Description of the study area.** The protected forest and fauna reserve known as the “Selva El Ocote” is located in the northwest portion of the state of Chiapas (16°53′–17°05′N and 93°30′–93°47′W) in the municipality of Ocozocoautla de Espinoza (Fig. 1). The reserve has an area of 48,140 ha (Diario Oficial de la Federación 1982) and ranges in altitude from 180 to 1500 m above sea level. The mean annual temperature and precipitation is 25.2°C and 2387 mm, respectively (INEGI 1984).

The soils of the reserve are thin and fragile, of limestone origin, with large numbers of exposed rocks and boulders (García et al. 1996). The topography is highly

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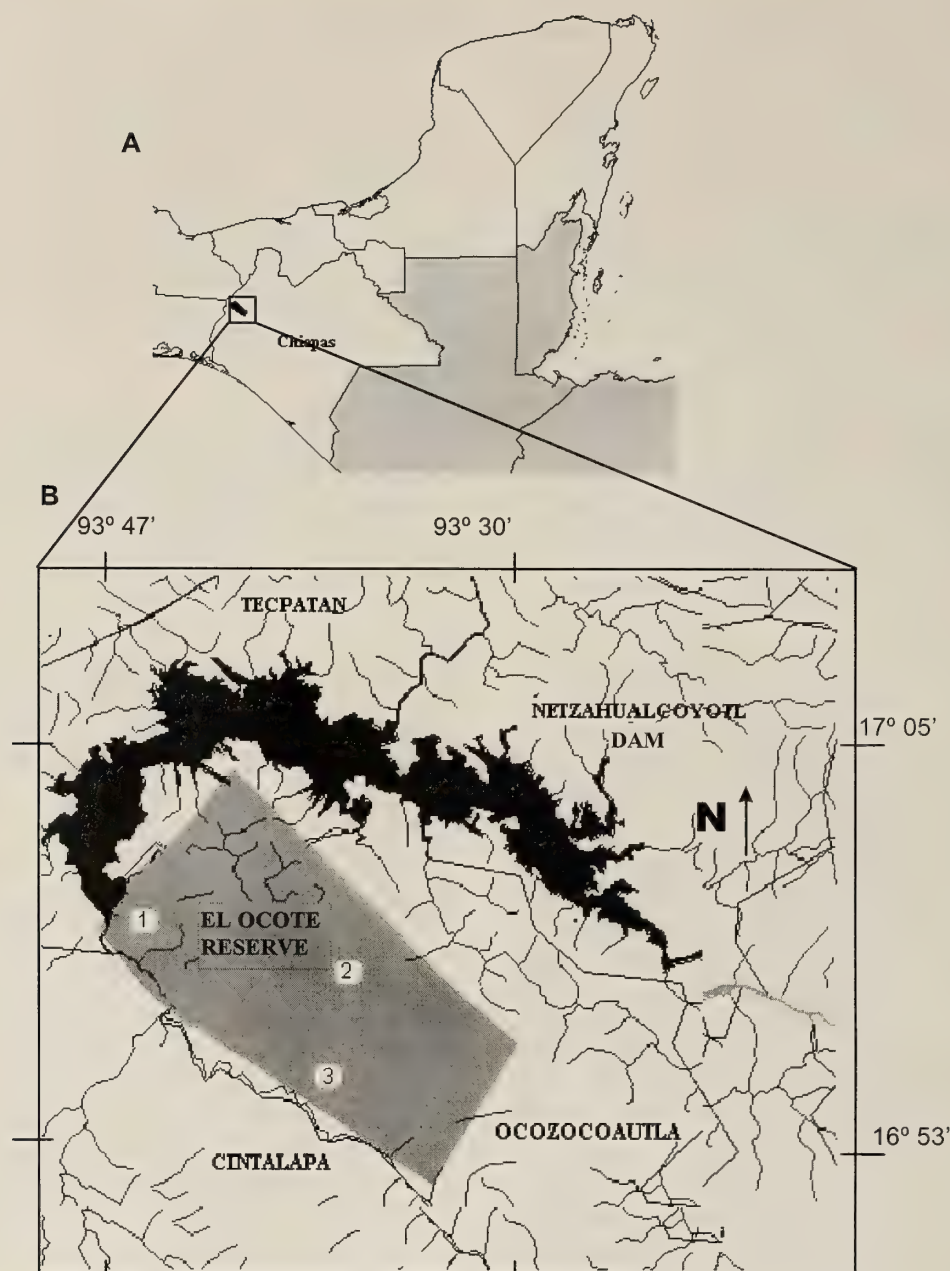


FIG. 1. A. Geographic position of the "El Ocote" Reserve in Southeastern México. B. Detail of the reserve and location of sampling areas: 1 = El Encajonado, 2 = 9 km SW of Ejido Cuauhtémoc 3 = Finca Nueva Providencia.

irregular and has contributed to the existence of very diverse floral assemblages, of which the high tropical semi-evergreen tropical forest is the dominant vegetation. This forest type coexists with fragments of medium height evergreen tropical forest, low semi-evergreen tropical forest, low deciduous tropical forest, and associated successional stages: "acahuales," savanna, and pastures (Ochoa-Gaona 1996).

**Sampling.** Night sampling was conducted at three locations that mostly comprised well preserved medium height evergreen tropical forest: El Encajonado, Ejido Cuauhtémoc and Finca Nueva Providencia (Fig. 1). These three locations provide a good representation of the spatial complexity of this type of tropical rain forest in the Reserve. Collections were mostly made during 1994. Supplementing field work

TABLE 1. Characteristics of the collection localities compared in this study. Vegetation categories are: TRF = Tropical Rain Forest, ESF = Evergreen Seasonal Forest, TDF = Tropical Deciduous Forest, and SS = Short-tree Savanna (Breedlove, 1981).

Locality	Elevation (m)	Latitude (N)	Longitude (w)	Mean annual temp.(°C)	Mean annual precipitation(mm)	Vegetation
"El Ocote", Chiapas	750	16°53'	90°30'	25.2	2387	TRF, EST, TDF SS
"Chajul", Chiapas	140	16°06'	90°55'	25.0	3000	TRF, ESF
"Los Tuxtlas", Veracruz	675	18°25'	90°13'	24.4	2900	TRF, TDF, ESF

was conducted in 1995, 1996 and 1997. Each collection coincided with the new moon and had an average duration of five days. A twelve volt ultraviolet light and sheet were placed from 1800 to 0500 h each night to attract moths. At the time of capture, each captured specimen was injected in the thorax with 95% ethyl alcohol and placed in individually labeled glassine envelopes. Species were identified using Hodges (1971), D'Abbrera (1986) and by comparison with reference material from the Entomology Collection of the Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM), in Mexico City. Collected specimens were deposited in the Entomology Collection of the El Colegio de la Frontera Sur, Unidad San Cristóbal, Chiapas (ECOSC-E) and the entomology collection of IBUNAM.

**Analysis of data.** Estimations of the species richness of the Sphingidae of "El Ocote" Reserve were based on the Clench equation of species accumulation:

$$S(t) = at / (1 + bt)$$

where  $S(t)$  is the expected number of species at time  $t$ ,  $a$  is the list increase rate,  $b$  is the species accumulation parameter, and the asymptote is given as  $a/b$  (Soberón & Llorente 1993). The model estimates total number of species present in the study area based on the characteristics of the decrease in new species collected as more time is spent in the field, this process will eventually generate an asymptote as an estimated total number of species (Soberón & Llorente 1993, León-Cortés 1995). The model was fitted by the non linear regression module provided by the package SPSS (v.6.1) using Levenberg-Marquardt algorithm.

The fauna of Sphingidae from "El Ocote" Reserve was compared with that reported for the Chajul Biological Station, Chiapas (León-Cortés & Pescador 1998) and Los Tuxtlas, Veracruz (Beutelspacher 1989) (Table 1), using the Simpson's similarity Index. This index is appropriate when compared faunas are disproportionate in size and number of shared taxa (Sánchez & López 1988). We applied cluster analyses using the unweighted arithmetic average clustering method

(UPGMA) to show the total relationships among these faunas (Crisci & López 1983).

## RESULTS AND DISCUSSION

**Species richness and seasonal abundance.** A total of 60 species of the family Sphingidae were collected from the "El Ocote" Reserve, belonging to three subfamilies, five tribes, and 20 genera (Table 2). The genus with the largest number of species was *Xylophanes* with 15 species, followed by *Manduca* with 10 species, and both *Eumorpha* and *Erinnyis* had five species each. These four genera represented 58% of the species collected in "El Ocote". León-Cortés and Pescador (1998) reported the same pattern in the abundance of species per genera from the Chajul Biological Station, in eastern Chiapas, and, in general, this also appears to be common to other tropical forests of America (León-Cortés & Pescador 1998).

The species collected from "El Ocote" Reserve represented 64% of the sphingids collected in the state of Chiapas and are all new records for the locality. Of these, *Nyceryx mulleri* Clark is a new state record. With our records, Chiapas has 49% of the Sphingidae reported from Mexico by White et al. (1991).

We estimated a species accumulation curve using Clench's equation. Our collection represents 75% of the Sphingidae of "El Ocote" Reserve predicted over 100 nights. Additional collection effort may provide only 10 to 15 more sphingid species (Fig. 2).

Three abundance categories were established using the criteria of Rabinowitz et al. (1986) and based on the numbers of specimens of each of the species collected. These categories were: "rare," (1 to 2 specimens); "common," (3 to 19 specimens); and "abundant," (20 to 50 specimens). Using these groupings, 16 of the collected sphingids were rare, 40 were common, and 4 were abundant (Table 2).

The number of species collected varied greatly between seasons. Forty-six species (77%) were only collected during the rainy season (May to October), whereas only one species was found exclusively during the dry season, as compared to 13 species (21%) which were found in both wet and dry seasons. Of the species



TABLE 2. List of species of Sphingidae (Insecta: Lepidoptera) collected in the "Selva El Ocote" Reserve in Chiapas, México during 1994–1997. F = February, A = April, M = May, J = June, Jl = July, Au = August, O = October and N = November, Total = Total number of specimens captured.

Species	Month	Total
<b>Subfamily Sphinginae</b>		
<b>Tribe Sphingini</b>		
<i>Cocytius lucifer</i> (Rothschild and Jordan, 1903)	Au	1
<i>Neococytius cluentius</i> Cramer, 1775	J	1
<i>Manduca dilucida</i> Edwards, 1887	M, J	4
<i>Manduca occulta</i> Rothschild and Jordan, 1903	F, M, J, O, N	12
<i>Manduca lefeburei</i> (Güerin, 1844)	M, J	5
<i>Manduca ochus</i> (Klug, 1836)	J, Jl	3
<i>Manduca rustica</i> (Fabricius, 1775)	M, J, O	10
<i>Manduca albiplaga</i> (Walker, 1856)	J	4
<i>Manduca muscosa</i> (Rothschild and Jordan, 1903)	J	4
<i>Manduca corallina</i> (Druce, 1883)	M	1
<i>Manduca lichenea</i> (Burmeister, 1856)	M, J, Jl, N	7
<i>Manduca florestan</i> Cramer, 1782	M, J, Jl	15
<i>Sphinx leucophaeta</i> Clemens, 1870	F	1
<i>Sphinx merops</i> (Boisduval, 1870)	F, M, J	4
<b>Subfamily Ambulicinae</b>		
<b>Tribe Smerinthini</b>		
<i>Protambulyx strigilis</i> (Linnaeus, 1771)	J, Jl, O	5
<i>Adhemarius gannascus</i> (Stoll, 1790)	M, J, Jl, Au, O, N	13
<i>Adhemarius ypsilon</i> Rothschild and Jordan, 1903	M, J, Jl, Au, O, N	20
<b>Subfamily Macroglossinae</b>		
<b>Tribe Dilophonotini</b>		
<i>Pseudosphinx tetrio</i> (Linnaeus, 1771)	J, Jl, Au, O, N	7
<i>Isognathus rimosus</i> Grote, 1865	M, J	4
<i>Erinnys alope</i> (Drury, 1770)	F, J	3
<i>Erinnys lassauxi</i> (Boisduval, 1859)	J	1
<i>Erinnys ello</i> (Linnaeus, 1758)	M, J	7
<i>Erinnys oenotrus</i> (Cramer, 1782)	M, J	10
<i>Erinnys obscura</i> (Fabricius, 1775)	M	1
<i>Pachylia ficus</i> (Linnaeus, 1758)	M, Jl	3
<i>Pachyliodes resumens</i> (Walker, 1856)	M, J	4
<i>Hemeroplanes ornatus</i> (Rothschild and Jordan, 1894)	M	3
<i>Hemeroplanes triptolemus</i> (Cramer, 1779)	F, M	1
<i>Madoryx oichus</i> (Cramer, 1779)	M, Jl	14
<i>Madoryx pluto</i> Cramer, 1779	M	1
<i>Callionima innus</i> (Rothschild and Jordan, 1903)	Jl	1
<i>Callionima parce</i> Fabricius, 1775	M, J, Jl, N	18
<i>Callionima falcifera</i> (Gehler, 1943)	F, J, Jl, Au, O	26
<i>Enyo lugubris</i> (Linnaeus, 1777)	M	1
<i>Enyo ocypete</i> (Linnaeus, 1758)	O	1
<i>Enyo gorgon</i> (Cramer, 1777)	A, M	2
<i>Perigonia lusca</i> Fabricius, 1777	M, J	5
<b>Subfamily Macroglossinae</b>		
<b>Tribe Philampelini</b>		
<i>Eumorpha anchemola</i> (Cramer, 1780)	M, J	3
<i>Eumorpha triangulum</i> Rothschild and Jordan, 1903	F, J, Jl, Au, O, N	10
<i>Eumorpha elisa</i> (Smyth, 1901)	J, Jl	8
<i>Eumorpha satellita</i> Linnaeus, 1771	F, J, Jl	25
<i>Eumorpha vitis</i> (Linnaeus, 1758)	M, J	4
<b>Subfamily Macroglossinae</b>		
<b>Tribe Macroglossini</b>		
<i>Cauthetia spuria</i> Boisduval, 1875	M, J, Jl	47
<i>Nyceryx mulleri</i> Clark, 1917	M	1
<i>Nyceryx riscus</i> Schaus, 1890	M	1
<i>Xylophanes pluto</i> (Fabricius, 1777)	M, J	3
<i>Xylophanes tyndarus</i> (Boisduval, 1875)	M, J	6
<i>Xylophanes pistacina</i> (Boisduval, 1877)	M, J	7
<i>Xylophanes porcus</i> (Hübner, 1829)	M, J	3
<i>Xylophanes ceratomiodes</i> (Grote and Robinson, 1867)	M, J, Au, O	8
<i>Xylophanes anubus</i> (Cramer, 1877)	J, Jl, Au	18
<i>Xylophanes amadis amadis</i> Stoll	J, Au	2
<i>Xylophanes amadis cyrene</i> (Druce, 1777)	J, Au	9
<i>Xylophanes belti</i> (Druce, 1878)	M, Jl	3
<i>Xylophanes eumedon</i> (Edwards, 1887)	J	2
<i>Xylophanes turbata</i> Edwards, 1887	M, J	4
<i>Xylophanes chiron nechus</i> Drury, 1770	M, J	7
<i>Xylophanes libya</i> (Druce, 1878)	M, J, Jl, A	10
<i>Xylophanes neoptolemus</i> (Stoll, 1782)	M, J, A, O	4
<i>Xylophanes thyelia</i> Linnaeus, 1758	O, N	4

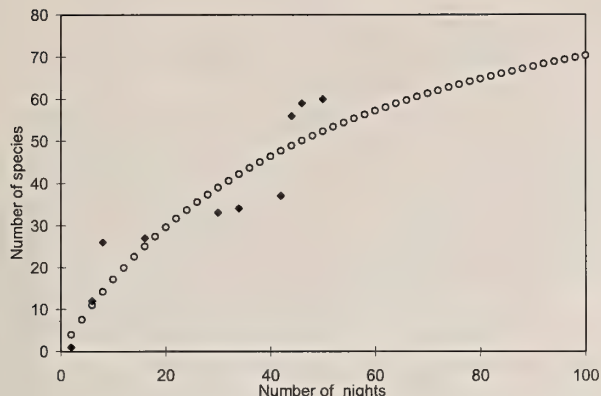


FIG. 2. Species accumulation curve of Sphingidae as a function of collection effort from "El Ocote", Reserve, Mexico. (○ = Cumulative number of expected species, (◆ = Cumulative number of observed species.

of sphingids collected during the rainy season, 48 of these (80%) were collected during the first two months of the season in May and June. Towards the end of the wet season, the abundance of each species declined and with fluctuations at low densities, in a manner similar to that observed during the dry season. This seasonal pattern in abundance and activity is similar to that reported in other studies (Haber & Frankie 1989, Janzen 1984, 1986, Powell & Brown 1990, Pescador 1994, Gregg et al. 1993). Haber and Frankie (1989) and Janzen (1984) state that precipitation and vegetative productivity are closely linked to the life cycle of the sphingids. During the dry season, the majority of the sphingids are in the pupal stage, while the larval and adult stages are found during the wet season. This pattern is reflected in reduced photosynthetic activity and productivity in host plants during the dry season, including the complete loss of leaves in some species, with the resumption of productivity during the wet season.

#### Similarity among fauna of the Sphingidae in Southern Mexico. The similarity among the sphingid

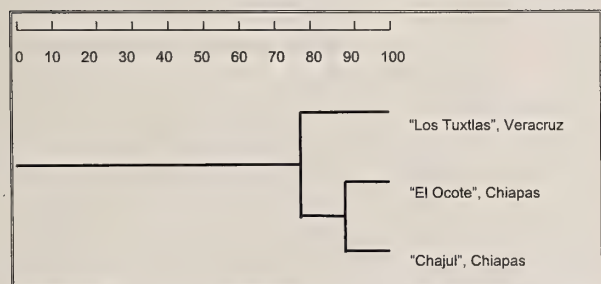


FIG. 3. Dendrogram of Sphingidae from three sites in southern Mexico. The unweighted arithmetic average (UPGMA) was used to cluster related groups.

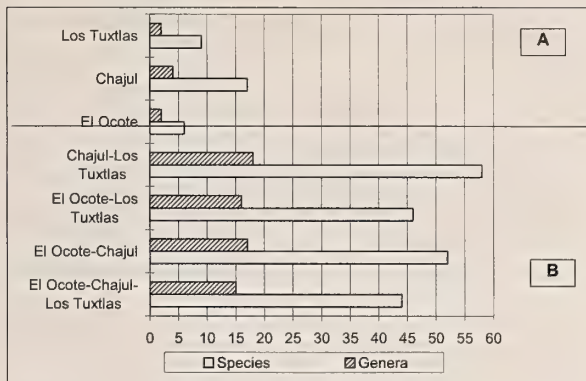


FIG. 4. Number of genera and species from the three localities compared from southern Mexico: A. number of genera and species not shared between sites, and B. number of genera and species shared between sites.

fauna at the three sites analyzed are presented in Fig. 3. Within the three localities, 29 genera and 100 species have been collected, of which only 15 genera and 44 species were shared. The dendrogram derived from the cluster analysis indicates that there is greater similarity between "El Ocote" and the "Chajul" region of the Lacandon Forest of eastern Chiapas, than with "Los Tuxtlas" located on the Gulf coast (Fig. 3). These two latter localities shared 18 genera and 58 species, whereas "El Ocote" shared 17 genera and 52 species with "Chajul" and 16 genera and 46 species with "Los Tuxtlas" (Fig. 4).

In 1998 forest fires devastated approximately 7.4% of "El Ocote" reserve during the National severe drought associated with the El Niño phenomenon of 1997 (Aguilera 1998). Since this study represents the only non-vertebrate faunal data available of the species richness of a specific group from the reserve before the fires, the data presented here may serve as a baseline for estimating the speed and nature of the recovery of the reserve following this major disturbance event. In addition, Sphingidae, being highly vagile species, easily monitored, and with relatively high diversity may be an especially appropriate group of organisms in the study of what is hopefully a process of recovery.

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## POLYPHENISM AND POPULATION BIOLOGY OF *EUREMA ELATHEA* (PIERIDAE) IN A DISTURBED ENVIRONMENT IN TROPICAL BRAZIL

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**ABSTRACT.** A population of *E. elathea* was studied for 13 months, from May 1996 to May 1997 in a disturbed environment in suburban Campinas, southeastern Brazil. The population showed fluctuations in numbers throughout the study period, with well-marked peaks of abundance in June–July, November–December and February. Sex ratio was male biased in four months and the time of residence was higher in the dry season. Both sexes were polyphenic; paler phenotypes occurred in the dry season and darker phenotypes in the wet season. Paler phenotypes were more frequently recaptured and had higher residence values than darker ones. Differences in behavior were attributed to adaptation to seasonally different environments.

**Additional key words:** Coliadinae, mark-recapture, urban butterflies.

The recent surge of interest in the conservation of tropical environments has led to an increase in studies of the natural history and ecology of organisms residing in the tropics (Noss 1996). These have included some long-term studies on population biology of neotropical butterflies, focused mainly on aposematic groups such as Heliconiini, Ithomiinae and Troidini (Turner 1971, Ehrlich & Gilbert 1973, Brown & Benson 1974, Drummond 1976, Young & Moffett 1979, Brown et al. 1981, Saalfeld & Araujo 1981, Vasconcellos-Neto 1980, 1986, 1991, Freitas 1993, 1996, Haber 1978, Rogner & Freitas 1999). Population studies with the Pieridae, however, have focused on non-tropical species, especially agricultural pests (Watt et al. 1977, 1979, Tabashnik 1980) common in this family (Chew 1995).

Seasonal polyphenism (Shapiro 1976, 1984) is an interesting feature of some pierid butterflies (the “whites” and “small yellows”). Numerous insect groups, especially butterflies, are polyphenic in response to seasonal abiotic factors (Shapiro 1976). Degree of melanization, number of wing spots (especially eye-like markings on the wings in Satyrinae), and color variations have been attributed to adaptation to seasonally different environments and thermoregulation (Shapiro 1976, Brakefield & Larsen 1984, Kingsolver & Wiernasz 1987, Braby 1994, Van Dyck et al. 1997, Windig et al. 1994). In general, seasonal morphs are related to dry vs. wet season in the tropics, and spring vs. summer or fall in temperate regions (Nylín 1989). Many different environmental factors induce polyphenism (see Shapiro 1984 and Jones 1992). Different behaviors linked to different color patterns also have been reported (Shreeve 1987, Nakasuji & Nakano 1990, Van Dyck et al. 1997).

The pierid *Eurema elathea* (Cramer, 1777) is a small Neotropical butterfly common in lawns, pastures, and other disturbed environments (DeVries 1987, Brown

1992). The polyphenism in this species was reported by Brown (1992), who noted that dry season forms were dorsally paler than wet season forms. The species is common on the Campus of the Universidade Estadual de Campinas (Unicamp), where it can be observed flying on the lawns and visiting several species of wild flowers (Oliveira 1996).

This paper provides a detailed account of the population parameters of *Eurema elathea*, and our objectives are to: (1) examine the age-structure, size and sex ratio and size of the population; (2) describe the variation in proportions of the different polyphenic types throughout the year; and (3) provide subsidies to the management of this species in urban habitats.

### MATERIALS AND METHODS

A mark-release-recapture (MRR) study was carried out on the Campus of the Universidade Estadual de Campinas (Unicamp), São Paulo state, southeastern Brazil, as part of a project of study of urban ecology on the Campus of the University. Annual rainfall is about 1360 mm and mean temperature 20.6°C (data from the Instituto Agronômico de Campinas). The regional climate is markedly seasonal, with a warm wet season from September to April and a cold dry season from May to August. During the research, the mean temperature of the coldest month was 17.6°C and of the warmest month was 24.8°C, with climate typical of the region (Fig. 1), except for May 1997, which was a rainy month and thus was included in the wet season.

The vegetation on the campus where the study was conducted consists of large lawns with sparse trees and scattered small flowering shrubs. The lawn was mowed five times during the period of study, as part of normal procedures of maintenance of the campus. The study area was divided into nine plots corresponding to lawns separated by walking trails connecting the buildings on the Campus (Fig. 2).

Butterflies were marked and recaptured between 28 May 1996 and 27 May 1997 (1–3 times per week), in

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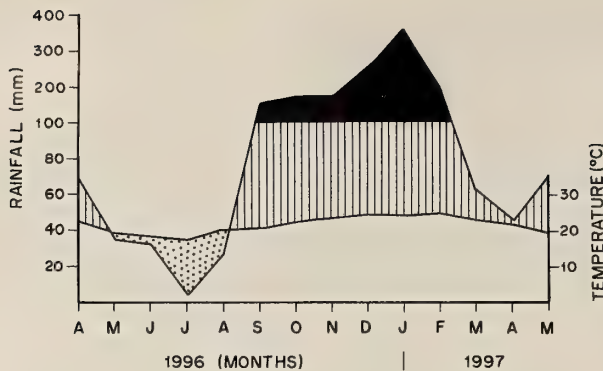


FIG. 1. Climagram for the Campinas region during the research (based on Santos 1965 and Walter 1985). Hatched = humid periods, black = superhumid periods, and dotted = dry periods.

sessions with 2–3 persons lasting 2–3 hours near mid-day, totaling 84 field days. The sessions ended when more than 80% of individuals captured represented recaptures of marks already given or recorded on that day.

Butterflies were net-captured, numbered on the underside of the forewings (felt-tipped pen), and released. Wing wear (seven “age” classes), point of capture, sex, forewing length and food sources were recorded (all following Freitas 1993, 1996, and Rogner & Freitas 1999). Forewing length was measured with a ruler, to the nearest mm. The age of individual butterflies was estimated in seven categories based on wing wear (Ehrlich & Davidson 1960, Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973), posteriorly grouped into three: new, intermediate and old (as in Freitas 1993, 1996 and Rogner & Freitas 1999). Values from one to seven, attributed to each wing wear class (where 1 = teneral and 7 = tattered) were used to compare the mean “age” of first captures in the different

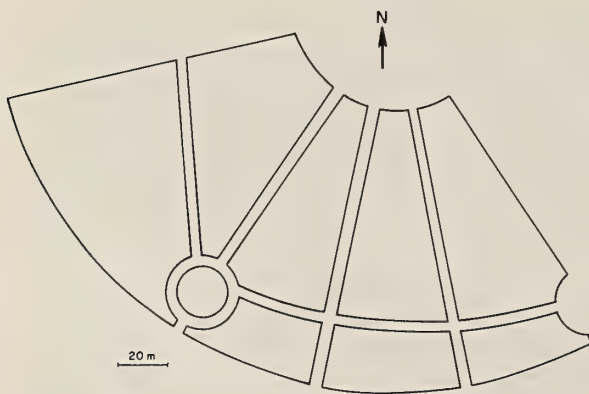


FIG. 2. Study area on the Campus of the Universidade Estadual de Campinas, showing the eight grassy areas (closed figures) separated by open trails. The small circular area, covered by dense shrubs (*Calliandra* sp., Fabaceae) was not sampled.

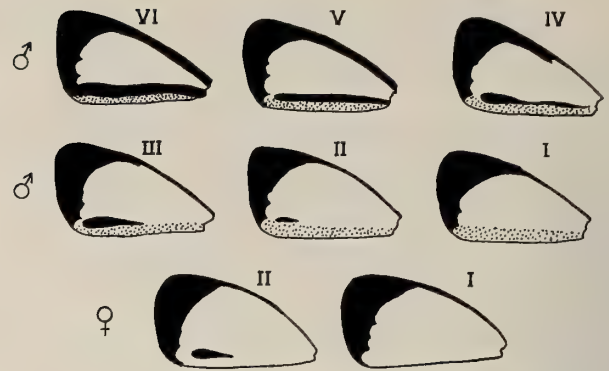


FIG. 3. Color types for males (top and middle rows) and females (bottom row) of *Eurema elathea* (background pale yellow, solid = black, dotted = orange).

color types. The amount of black on the dorsal forewing inner margin was recorded for males and females (details in next section).

The mark-release-recapture (MRR) data were analyzed by the Jolly-Seber (Southwood 1971) method for estimating population parameters (CMLR software developed by Dr. R. B. Francini, Unisantos) for the obtainment of estimated population numbers and standard errors. Daily results were tabulated as “number of individuals captured per day” (NICD), and “number of individuals present per day” (NIPD). To estimate the NIPD, recaptured individuals were considered to be present in the population on all previous days since the day of first capture (=marked animals at risk) (following Rogner & Freitas 1999). The data were grouped for analysis into “dry season” (May–August 1996) and “wet season” (September 1996–May 1997), in accord with the rainfall (climagram in Fig. 1).

**Phenotype.** Males were classified in six color types (I to VI) based on the amount of black on the dorsal forewing inner margin (Fig. 3), following a classification used previously by Ruszczyk and collaborators (unpublished data) for *E. elathea* in central Brazil. The extremes were “marginal black bar absent” (type I)

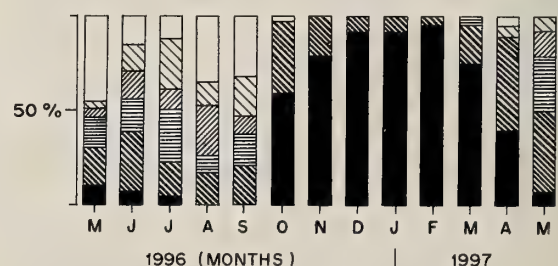


FIG. 4. Monthly percent of different male color types of *E. elathea* from May 1996 to May 1997. From top to bottom in first column, types I to VI.

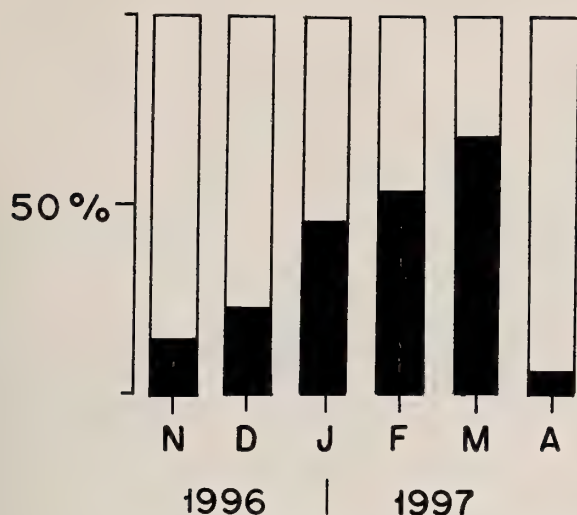


FIG. 5. Monthly percent of different female color types of *E. elathea* from May 1996 to May 1997. White = type I (pale), black = type II (dark). Because the type II was absent from May to October 1996, the first six months were combined in a single bar.

and “broad and complete marginal black bar” (type VI). In females only two color types were defined: “marginal black bar absent” (type I) and “short marginal black bar” (type II). Intermediates, as defined by the length and width of the black stripe, were not observed in females. The variation appeared to be continuous in males, causing some problems in defining the classes of intermediates especially in the first month (the first 40 individuals marked were discarded), resulting in a total number of assigned polyphenic types different from the total by sex.

## RESULTS

**Phenotype.** Males of the color types I to IV were more common in the dry season, and V and VI were more common in wet season. The latter two phenotypes (dark forms) represented 90–100% of the total individuals seen in seven months (all in the wet season), and less than 50% in the other months (two in the wet season and all dry season months) (Fig. 4). Females of the color type II (the dark wet season form) appeared first in November 1996, disappearing after April 1997 (Fig. 5). The proportions should be compared with the climate of the previous month, when the individual completed larval growth and pupated. Thus, although September was a wet month, the proportion of lighter forms was very high, reflecting the dry weather of August; and even though April was relatively dry, the darker forms still predominated (Fig. 1).

**Population biology.** In all, 1468 individuals of *Eurema elathea* were captured during the 12 months of

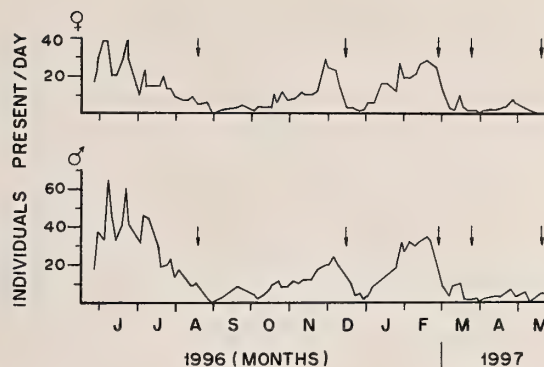


FIG. 6. Number of individuals present per day (NIPD) of males (below) and females (above) of *E. elathea* from May 1996 to May 1997. Arrows indicate mechanized grasscuttings.

the study, with 320 of these recaptured at least once. In the dry season (25 days), the number of individuals captured per day varied from 0 to 53 individuals (mean = 21.3; SD = 14.3) for males and 0 to 32 (mean = 13.6; SD = 8.2) for females. In the wet season (59 days), the number of individuals captured per day varied from 0 to 32 individuals (mean = 9.8; SD = 8.4) for males and 0 to 27 (mean = 7.9; SD = 7.8) for females. The number of individuals present per day in the dry season varied from 0 to 64 individuals (mean = 27.9; SD = 17.2) for males and 0 to 39 (mean = 17.6; SD = 11.0) for females. In the wet season, the same varied from 0 to 35 individuals (mean = 11.0; SD = 9.6) for males and 0 to 29 (mean = 8.7; SD = 8.7) for females. The population (based on NIPD) presented three peaks of abundance for both sexes: June–July 1996, November–December 1996 and February 1997 (Fig. 6). Mechanized grasscuttings (17 Aug. 1996, 13 Dec. 1996, 27 Feb. 1997, 23 Mar. 1997 and 17 May 1997, arrows in Fig. 6), led to decrease in adult abundance especially in 1997 after three grasscuttings at 24 and 55-day intervals.

Males were recaptured up to six times in the dry season and up to four times in the wet season; females were recaptured up to four times in dry season and up to three times in wet season. In all, 200 males and 120 females were recaptured at least once (Table 1). The highest recapture rate was observed in male color type I (dry season), and the lowest in male color type VI (wet season) and in both female color types (Table 2). Multiple recaptures were significantly more frequent in males (Table 2). The results of Jolly-Seber analysis for males and females separately (Figs. 7 and 8) show patterns very similar to those of NIPD (Fig. 6).

The total sex ratio (809 males and 659 females) was male biased ( $\chi^2 = 15.3$ ,  $df = 1$ ,  $p < 0.001$ ), but when



TABLE 1. Recapture rates of adults of *Eurema elathea* in the study. cap = total captured, recap = individuals captured at least once. Asterisks on the Chi square values indicate that the difference is significant ( $P < 0.05$ ,  $df = 1$ ). Chi squares were calculated considering "cap" versus "individuals never recaptured" ("cap" minus "recap").

Sex	Dry		Wet		Total	
	cap/recap	%	cap/recap	%	cap/recap	%
Males	370/104	28.1	439/96	21.9	809/200	24.7
Females	265/59	22.3	394/61	15.5	659/120	18.2
Total	635/163	25.7	833/157	18.8	1468/320	21.8

**Chi squares**

males vs females	$\chi^2 = 2.78$	$\chi^2 = 5.39^*$	$\chi^2 = 9.03^*$
dry vs wet	$\chi^2 = 9.27^*$		

the months were analyzed separately, significant bias was observed in only four months (June, July and December 1996, and May 1997), with females dominating only in one month and sex ratio nearly 1:1 in four months (Fig. 9). Although the proportion of recaptures of males was higher than females, differences were significant only in the wet season, with total recapture rate significantly less than in the dry season (Table 1).

**Age structure and residence time.** Most of the first captures of both sexes were individuals of "intermediate" age (49% of males and 52% of females). Based on the categories of wing wear, the "age" of first recapture of males (mean class = 2.65, SD = 0.86,  $n = 744$ ) was lower than females (mean = 2.83, SD = 0.87,  $n = 660$ ) ( $t = 4.0$ ,  $df = 1402$ ,  $p < 0.0001$ ). Color type VI was captured at a lower "age" than all other types except I (Table 2). The population showed peaks in abundance of "new" individuals in late June, Au-

TABLE 2. Population parameters of the different color types of *Eurema elathea*. Different superscript letters show significant differences among the different phenotypes. AFC = mean age at first capture (based on age categories), MRT = mean residence time (days), MUR = proportion of individuals with multiple recaptures (%), MOV = proportion of individuals that moved to another subarea (%).

	Males				Females			
	I	II	III	IV	V	VI	I	II
Marked	64	62	47	70	146	355	529	131
Recaptured	24	14	12	19	40	76	95	25
% of recapture*	37.5 <sup>a</sup>	22.6 <sup>ab</sup>	25.5 <sup>ab</sup>	27.1 <sup>ab</sup>	27.4 <sup>ab</sup>	21.4 <sup>b</sup>	17.9 <sup>b</sup>	19.1 <sup>b</sup>
AFC**	2.77 <sup>ab</sup>	2.86 <sup>a</sup>	2.89 <sup>a</sup>	2.78 <sup>a</sup>	2.89 <sup>a</sup>	2.43 <sup>b</sup>	2.77 <sup>a</sup>	2.85 <sup>a</sup>
MRT								
(days)***	11.4 <sup>a</sup>	10.5 <sup>a</sup>	8.6 <sup>a</sup>	12.0 <sup>a</sup>	9.0 <sup>a</sup>	10.2 <sup>a</sup>	7.5 <sup>a</sup>	9.1 <sup>a</sup>
MUR	45.8	35.7	25.0	52.6	35.0	32.9	21.0	16.0
MOV	83.3	57.1	75.0	73.7	80.0	75.0	61.0	76.0

\*  $p < 0.05$ , Chi-square tests

\*\*  $p < 0.05$ , one way ANOVA

\*\*\*  $p > 0.05$ , one way ANOVA

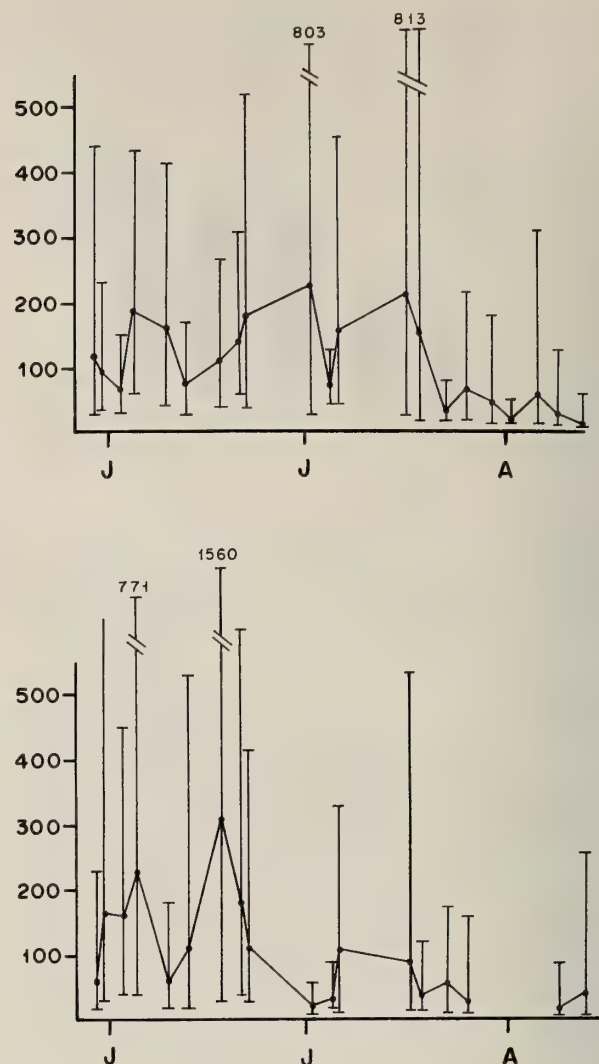


FIG. 7. Estimated population size (Jolly-Seber) for *E. elathea* males (above) and females (below), from May to August 1996. The maximum number of individuals is given as the estimate plus the error (superior part of vertical bars), and the minimum number is given as the number of individuals present per day (inferior part of vertical bars), assuming that the population could not be lower than this number.

gust–September, late November and February, suggesting high rates of recruitment in these periods (Fig. 10), with some indication of protandry.

Combining both seasons, residence time of males (mean = 9.8 days, SD = 7.7,  $n = 201$ ) was not significantly higher than that of females (mean = 8.3 days, SD = 7.6,  $n = 119$ ) ( $t = 1.710$ ,  $df = 318$ ,  $p = 0.09$ ). However, differences were significant in the wet season ( $t = 2.127$ ,  $df = 155$ ,  $p = 0.03$ ), and not in the dry season ( $t = 0.749$ ,  $df = 161$ ,  $p = 0.45$ ). Residence times were marginally higher in the dry season for both males ( $t = 1.95$ ,  $df = 199$ ,  $p = 0.052$ ) and females ( $t =$

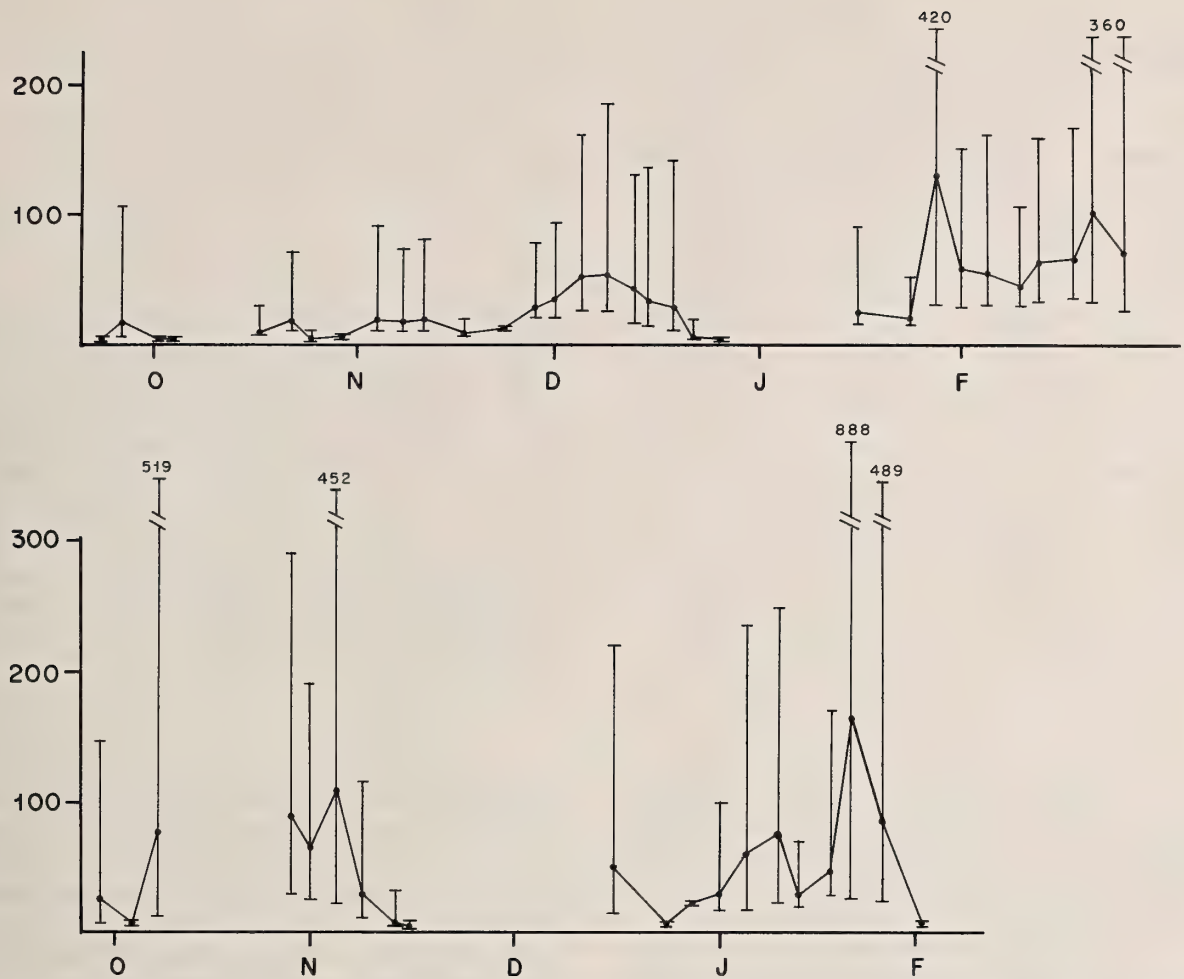


FIG. 8. Estimated population size (Jolly-Seber) for *E. elathea* males (above) and females (below), September 1996 to February 1997 (see Fig. 7 legend).

1.99,  $df = 117$ ,  $p = 0.049$ ) (see also Table 3). The maximum residence time in the dry season was 52 days for a male and 54 days for a female, and in the wet season 28 days for a male and 21 days for a female. The residence times were not different among the different phenotypes of males and females ( $F_{7,297} = 0.903$ ,  $p = 0.504$ ) (Table 2). Survival of males and females in each

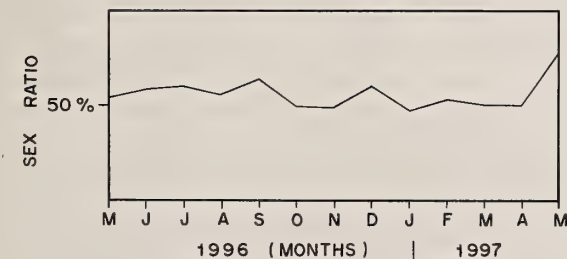


FIG. 9. Sex ratio for *E. elathea* from May 1996 to May 1997, as percent of males in each day's captures.

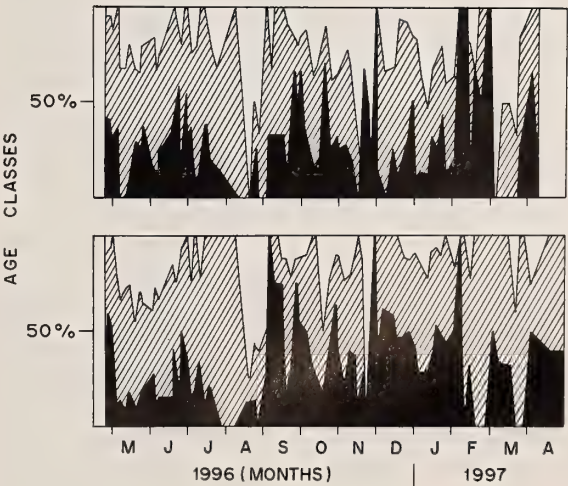


FIG. 10. Age structure of males (below) and females (above) of *E. elathea* (black = fresh individuals, hatched = intermediate, white = worn individuals) from May 1996 to May 1997.



TABLE 3. Residence time (in days) of *Eurema elathea* adults in the dry and wet seasons. Days elapsed between marking and last recapture represent the minimum permanence (MP) for each individual.

MP (days)	Males (%)	Females (%)	Total (%)
<b>Dry Season</b>			
1-5	36 (34.6)	29 (49.1)	65 (39.9)
6-10	23 (22.1)	12 (20.3)	35 (21.5)
11-15	22 (21.1)	5 (8.5)	27 (16.5)
16-20	8 (7.7)	4 (6.8)	12 (7.4)
21-25	8 (7.7)	4 (6.8)	12 (7.4)
26-30	2 (1.9)	4 (6.8)	6 (3.7)
31-35	3 (2.9)	—	3 (1.8)
> 35	2 (1.9)	1 (1.7)	3 (1.8)
Total	104	59	163 (100)
Mean $\pm$ sd	10.9 $\pm$ 9.1	9.7 $\pm$ 9.8	
Max	52	54	
<b>Wet Season</b>			
1-5	34 (35.4)	32 (52.4)	66 (42.0)
6-10	33 (34.4)	15 (24.6)	48 (30.6)
11-15	16 (16.7)	11 (18.0)	27 (17.2)
16-20	9 (9.4)	2 (3.3)	11 (7.0)
21-25	2 (2.1)	1 (1.6)	3 (1.9)
26-30	2 (2.1)	—	2 (1.3)
Total	96	61	157 (100)
Mean $\pm$ sd	8.8 $\pm$ 5.6	6.9 $\pm$ 4.2	
Max	28	21	

season are somewhat different (Table 3), with estimated median residence time ("life expectancy" of Cook et al. 1967) of 5.53 days for males and 4.72 days for females in the dry season, and 4.95 days for males and 4.87 days for females in the wet season.

**Forewing length.** For the entire sample, the average forewing length of females (mean = 17.9 mm, SD = 1.19,  $n = 661$ ) was statistically greater than males (mean = 17.4 mm, SD = 1.05,  $n = 782$ ) ( $t = 7.51$ ,  $df = 1441$ ,  $p < 0.001$ ), and this difference was significant in seven months (Table 4). No significant differences in wing length were observed among the different color

TABLE 4. Mean forewing length ( $\pm$  SD) of *Eurema elathea* in this study. Asterisks indicates that means are different between sexes in that month ( $t$ -tests,  $p < 0.05$ ).  $N$  = sample size.

Month/year	Males	N	Females	N
May/1996*	17.6 $\pm$ 0.9	60	18.4 $\pm$ 1.2	52
Jun/1996*	17.4 $\pm$ 1.1	147	17.9 $\pm$ 1.1	108
Jul/1996*	17.3 $\pm$ 1.1	111	17.9 $\pm$ 1.3	72
Aug/1996	17.2 $\pm$ 1.4	32	17.8 $\pm$ 1.3	32
Sep/1996	17.8 $\pm$ 1.1	19	18.1 $\pm$ 1.4	11
Oct/1996*	16.7 $\pm$ 0.9	39	17.3 $\pm$ 1.0	38
Nov/1996*	17.1 $\pm$ 1.1	60	17.5 $\pm$ 1.1	62
Dec/1996*	17.3 $\pm$ 0.8	58	17.9 $\pm$ 1.2	40
Jan/1997*	17.3 $\pm$ 0.9	65	17.9 $\pm$ 1.2	74
Feb/1997	17.7 $\pm$ 0.9	133	17.8 $\pm$ 1.2	120
Mar/1997	17.8 $\pm$ 0.8	24	18.0 $\pm$ 1.2	25
Apr/1997	17.8 $\pm$ 0.9	20	17.9 $\pm$ 1.1	23
May/1997	17.5 $\pm$ 1.2	14	17.0 $\pm$ 1.4	4

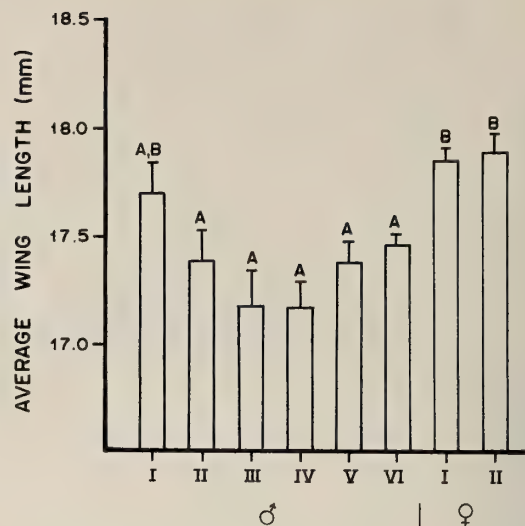


FIG. 11. Mean ( $\pm$  SD) forewing length of males and females of *E. elathea* (based on monthly recruitment). Different letters above the bars indicate significant differences in the means (one way ANOVA,  $p < 0.005$ ).

types within sexes (Fig. 11). Average wing length of males was equal in the dry (mean = 17.4 mm, SD = 1.11,  $n = 350$ ) and the wet season (mean = 17.4 mm, SD = 0.99,  $n = 432$ ) ( $t = 0.942$ , SD = 780  $p = 0.34$ ). In females, average wing length in the dry season (mean = 18.0 mm, SD = 1.21,  $n = 264$ ) was considered greater than in the wet season (mean = 17.8 mm, SD = 1.17,  $n = 397$ ) ( $t = -2.437$ ,  $df = 659$ ,  $p = 0.015$ ).

**Natural history of the adults.** Adults started activity around 0800 h in summer and 1000 h in winter, varying greatly with the weather (on some cold days during winter, the activity only began after 1100 h). As a rule, the peak of activity of the adults was between 1200 h and 1400 h, especially in the wet season, when many individuals were in courtship behavior or mating, and females usually were looking for plants for oviposition. After 1600 h, activity diminished, and especially in the dry season, the butterflies congregated in some grass patches in the study area to roost in loose aggregations.

Movements among the subareas were observed in all color types of both sexes. Males of color types I and V had the greatest number of individuals moving between sub-areas (Table 2). In the dry season, butterflies appeared to be more resident, engaging mainly in short flights, while in the wet season they were more active and frequently observed in long flights. Due to the fact that the different subareas were of unequal size, the proportions of individuals moving to other subareas do not reflect the flight distances.

Adults were usually seen feeding on flowers. Thirteen species of flowers were used as nectar sources. The most visited was *Emilia sonchifolia* (Asteraceae) (103 of a total of 150 records), but virtually any plant species in blossom was observed being used by the adults (see Oliveira 1996 for a list of flowers used in this same area).

#### DISCUSSION

**Population biology.** Male biased sex ratios have been observed in many natural populations of butterflies, even when the sex ratio in laboratory was 1:1 (e.g., Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973, Brussard et al. 1974, Watt et al. 1977, 1979, Brown & Ehrlich 1980, Ehrlich 1984, Ehrlich et al. 1984, Matsumoto 1984, 1985, Freitas 1993, 1996). Behavioral differences may contribute to this bias (Ehrlich 1984, Freitas 1996); Shapiro (1970) argues, however, that in several pierids this bias is related to the density of males. In this study, females accounted for 44.9% of the 1468 individuals collected in one year (male:female ratio 1.2:1), but the ratio was different from 1:1 in only four months.

Residence time of *E. elathea* is not high if compared to tropical butterflies in the genus *Heliconius* (Turner 1971, Benson 1972, Ehrlich & Gilbert 1973), but is similar to that obtained for some Ithomiinae (Vasconcellos-Neto 1980, Freitas 1993, 1996, Rogner & Freitas 1999). Dispersal of adults probably affects residence time, explaining the lower time of residence, mainly in the wet season. Especially the lower residence time of females in the wet season could be related to higher dispersal rates in this sex (see also Shapiro 1970 and Freitas 1993, 1996). Increased dispersal after the first rains has been reported in Ithomiinae in tropical seasonal forests (Vasconcellos-Neto 1980).

Also contrasting with populations of *Heliconius* butterflies, that maintain relatively constant numbers throughout the year (Turner 1971, Ehrlich & Gilbert 1973, Araujo 1980, Rogner & Freitas 1999), *E. elathea* fluctuated markedly in abundance throughout the year, in a way similar to that observed in Ithomiinae (Nymphalidae) and Troidini (Papilionidae) (Brown & Benson 1974, Drummond 1976, Haber 1978, Young & Moffett 1979, Vasconcellos-Neto 1980, 1986, 1991, Brown et al. 1981, Freitas 1993, 1996). Such fluctuations may be common in populations of temperate-zone pierids (Watt et al. 1977, 1979, Tabashnik 1980). For *E. elathea* in this study, these fluctuations are in part related to local grasscuttings, which probably destroyed many immatures, and made the adults leave the area looking for food sources. In the present work,

grasscuttings occurred in periods of population decline, on all occasions (Fig. 6), affecting the population and leading to very low numbers of butterflies in May 1997. Recolonization of the area probably occurred by individuals arriving from nearby populations, and the increase in the frequency of intermediate and old individuals after the first grasscutting (on 17 August 1996) supports this idea. The high proportion of first captures of individuals classified as intermediate and old suggests that migration might be common among subpopulations, and could provide new stock to a recently cut site. These population features suggest that this butterfly species would persist in metapopulations (Hanski & Gilpin 1997) in the study area. Further investigation on this subject could reveal important patterns in the ecology of butterflies in urban environments, but the results suggest that grasscuttings should be done after the first rains, when the population starts to be more vagile. Also, the grasscuttings in the dry season destroyed the roosting places of the butterflies, that could affect the survival of the individuals in the dry environment.

Even if reproductive diapause was not investigated in the present study, some comparisons can be made with other butterfly species in the seasonal tropics. Several species of tropical butterflies are known to exhibit reproductive seasonality (e.g., Jones & Rienks 1987, Braby 1995), and this pattern is supposed to be linked with rainfall, and consequently with the availability of host plants (Braby 1995). The pattern observed in *E. elathea* in the present study is similar to that exhibited by *E. hecabe* in Australia (Jones & Rienks 1987), with the maximum populational density reached in the middle of the dry season (but the effects of lawn mowing, that is affecting the population numbers, cannot be discarded). In *E. hecabe*, "gravid" females were present in all samples, but the proportion of them dropped when the population reached a peak (Jones & Rienks 1987). Thus, we could hypothesize that if *E. elathea* follows the same pattern, the population of this species present continuous breeding, but the number of reproductive females in the dry season (also the population peak) might be low. This subject is now under investigation by Ruszczyk and collaborators in a population in central Brazil.

**Polyphenism.** In most studies of polyphenic species of butterflies, dry-season phenotypes were lighter and less conspicuous than wet-season phenotypes (Brakefield & Larsen 1984, Shapiro 1984, Brakefield 1987, Brakefield & Reitsma 1991, Jones 1992, Braby 1994, Windig et al. 1994). These differences have been related to ventral surface camouflage in the more sedentary color morphs produced in the dry sea-



son (Shapiro 1976, Brakefield & Larsen 1984, Brakefield & Reitsma 1991, Jones 1992, Van Dyck et al. 1997). In the present study, paler phenotypes were also more frequent in the dry season, when a brown substrate of dead leaves predominated on the ground where the butterflies rest. This paler phenotype may enhance survival of *E. elathea* through crypsis as the environment dries out and changes color (Owen 1971, Jones 1987, 1992). Thus, the different phenotypes could represent responses to seasonal differences in the environment and selective pressures such as predation (Brakefield & Larsen 1984, Brakefield 1987, Brakefield & Reitsma 1991). Braby (1994) proposed that in satyrs, dark wet-season forms rely on anti-predator devices (prominent eyespot patterns) which are displayed at rest and function to deflect attacks; while lighter dry-season forms with reduced eyespots probably rely on crypsis for survival. Windig et al. (1994) proposed that selection on males tends to favor wing patterns contributing positively to mate-seeking activity and thermal budgets (small and dark wings), while selection on females tends to favor paler ground colors and, in wet season forms, conspicuous markings (as female type II in this study). Allied with differences in color and pattern, differences in behavior in different seasons and phenotypes were observed on several occasions (Guppy 1986, Shreeve 1987, Nakasuji & Nakano 1990, Van Dyck et al. 1997). A possible hypothesis to be tested in tropical seasonal environments is that paler dry-season forms would be more resident than darker wet-season forms, that could enhance the value of their cryptic coloration (as reported in Van Dyck et al. 1997). The results of recapture rates of males of different color types of *E. elathea* in this study agree with this, since the paler color type (type I) had a higher recapture rate, and the darker color type (type VI) had a lower recapture rate (see Table 2). Unfortunately, the present study does not provide real distances traveled by the individuals, due to the fact that the different subareas were of unequal size (Fig. 2), and the hypothesis that paler phenotypes are more resident could not be tested.

Behavioral differences among the different color types could also be related to wing melanization (and, consequently, to thermoregulation) and body size (wing length). Van Dyck et al. (1997) hypothesize that small phenotypic wing differences could result in considerable variation in thermoregulation: darker butterflies could heat up more rapidly (Wasserthal 1975), and could spend more time flying and searching for females. In the study area, the wet season is also the warm season, and dark butterflies probably would become warm faster than pale forms, resulting in in-

creased flight activity. This could be true in many tropical seasonal habitats. If this holds, dark butterflies would benefit in all seasons (warm or cool), and their absence or low numbers in the dry season would be explained only by the cryptic advantage of the paler forms in dry season. Future research in this subject is needed to investigate this point.

The ventral pattern of the wings (not analyzed in this study) varies continually from plain white (mostly in the wet season) to patterned yellow and orange (mostly in the dry season) in both sexes. This is the side normally displayed by the butterflies at rest; the variation probably enhances camouflage and thermal effects in the different color types. Ruzsarczyk (pers. comm.) proposed that when *E. elathea* males are flying, the black bar of the darker types resembles the black bar of the hindwing outer margin of the distasteful moth *Utetheisa ornatatrix* (Arctiidae). The white pattern of the underside of these morphs also matches the light coloration of this moth. The two species often fly together and use similar substrates when perched, and this could be a good hypothesis to be investigated in the future.

Size is also important, since larger butterflies could more easily attain and maintain higher temperatures (Willmer & Unwin 1981). Van Dyck et al. (1997) propose that larger darker individuals would be adapted for patrolling and dispersal. Dry-season forms are in general larger than wet-season forms (Brakefield 1987, Brakefield & Reitsma 1991, Jones 1992, Braby 1994). Brakefield and Reitsma (1991) argue that this difference could be the result of behavioral and life history components: larger butterflies were the result of opportunistic development at the end of the wet season, while dry season forms derived more benefit from fast development (resulting in smaller size) which enables their progeny to complete development before the vegetation dries out. In most pierids, larger adults arise when larvae are reared at lower temperatures, and in two *Eurema* species larger size was induced by short photoperiods (Jones 1992). In this study, no significant differences in size in *E. elathea* were observed within the different color types, but the dry season females were larger than wet season females (not wet season forms). According to Braby (1994), several advantages could be associated with this increase in size, like increased longevity and capacity of storage in the fat body, both important in the dry season, when food resources are scarce.

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## GENERAL NOTES

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### IS SPERMATOPHORE NUMBER A GOOD MEASURE OF MATING FREQUENCY IN FEMALE *CALLOPHRYS XAMI* (LYCAENIDAE)?

**Additional key words:** copulation, female remating, mating system.

Recent developments in sexual selection theory suggest that the role of females in shaping the evolution of mating systems has been underestimated (Eberhard 1996). In particular, female mating frequency is considered a variable that affects the potential for, and the strength of, sperm competition (Drummond 1984) and cryptic female choice (Eberhard 1985, 1996). In Lepidoptera, spermatophore counts have been used to determine the number of times a female has mated (Burns 1968, Drummond 1984, Eberhard 1985). However, the validity of spermatophore number as a measure of female mating frequency is based upon a number of assumptions which need to be verified before inferences about mating systems are made (Burns 1968, Lederhouse et al. 1989, Braby 1996). Here, I report the number of spermatophores found in a field sample of females of the lycaenid butterfly *Callophrys xami* (Reakirt); and, based upon previous information on the mating behavior and spermatophore production patterns in this butterfly (Cordero 1993, 1998), I discuss possible biases incurred when using such a measure as an estimate of female mating frequency.

I sampled females during eight sunny days, between 28 December 1989, and 23 January 1990 (this multivoltine species reaches its highest density between October and January (Soberón et al. 1988)) in the Pedregal de San Angel ecological reserve, located in the south of Mexico City (description of the area in Soberón et al. 1988). All females observed during these days were collected and frozen until dissection. I measured the length of the right forewing of each female with a calliper. I used this length as a measure of body size, considering that there was a positive correlation between wing length and body weight in a laboratory-reared sample of females ( $r = 0.8$ ,  $p < .001$ ,  $n = 27$ ). I also determined the degree of female wing wear using the following scale: (1) similar to a recently emerged adult (wings mostly green on the ventral side with intact margins), (3) very worn female (wings mostly brown on the ventral side with worn margins), and (2) all individuals intermediate between (1) and (3). I evaluated the frequency of "successful" copulations by females (i.e., copulations that resulted in spermatophore transfer) by counting the number of spermatophores and spermatophore remains in the corpus bursae.

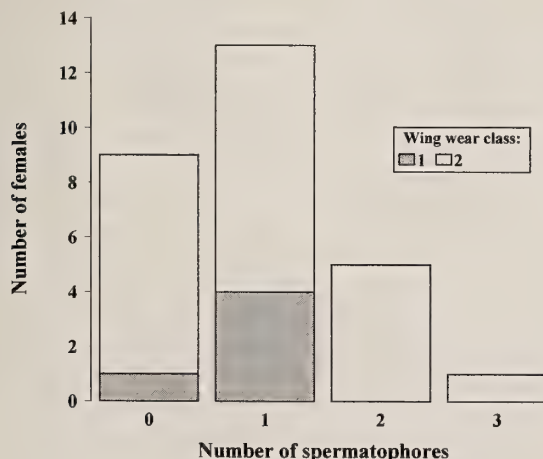


FIG. 1. Distribution of females with different number of spermatophores and the relationship between number of spermatophores and wing wear category.

The number of spermatophores in the 28 females I collected ranged from 0 to 3 (Fig. 1). The percentage of females without spermatophores was 32.1%, with one spermatophore was 46.4%, and with more than one spermatophore was 21.4%. The mean  $\pm$  SD number of spermatophores found in females with at least one spermatophore was  $1.37 \pm 0.6$ . I looked for a relation between female wing length and spermatophore number with Spearman correlation because wing length was not normally distributed. This correlation was not significant ( $r_s = -0.07$ ,  $p > 0.05$ ,  $n = 27$ ). Since all females collected were in wing wear conditions 1 or 2, I compared the number of spermatophores of females in each condition with a Mann-Whitney  $U$  test without finding significant differences ( $U = 54$ ,  $p > 0.05$ ; Fig. 1).

Since the work of Drummond (1984) is the only extensive summary presenting data from Lycaenidae, I use the data in that paper as a reference. Considering average number of spermatophores per mated female, maximum number of spermatophores, and proportion of females multiply mated, female Lycaenidae relative to other lepidopterans show the lowest degree of polyandry, comparable only with the Satyrinae (Drummond 1984). However, *C. xami* shows some differences when compared with the four lycaenid species included in Drummond (1984). The average copulation frequency estimated for mated females ( $1.37 \pm 0.6$ ), the maximum number of spermatophores (3), and the proportion of females multiply mated (21.4%) in *C. xami* is higher than in the other four lycaenids (ranges of average copulation frequency values: 1.05–1.17; maximum number of spermatophores: 2 in the four species; and proportion of females multiply mated: 3.7–12.7%). Furthermore, average number of copulations, maximum number of spermatophores, and proportion of females multiply mated could be underestimated in *C. xami*, since no females in the very worn ("old") wing wear condition were collected (Fig. 1). A sampling bias could exist if "old" females were more difficult to detect or to capture. However, our research group has been studying this species in the field for more than 10 years, and we have no evidence of any greater difficulty in observing and catching "old" females. It is possible that most females do not live long enough to become very worn and, therefore, are rare; in this case our estimates of copulation frequency would be unbiased. On the other hand, since outside the sampling period we have observed very worn *C. xami* females in the field, it is also possible that the abundance of "old" females varies in time as a result of, for example, varying predation pressure or weather conditions. Under these conditions, average and maximum number of spermatophores could vary with time depending on the age structure of females.

The method used to evaluate female copulation frequency in the field is based on three assumptions (modified from Drummond 1984):

**Copulation always results in spermatophore transfer.** In *C. xami* this is not true because there are some copulations of very short duration that do not result in the transfer of a spermatophore (Cordero 1993, 1998). However, these "interrupted" copulations are not common in the field (0/18 copulations observed in 1983–1985 and 2/27 copulations observed in 1989–1990; Cordero 1993). On the other hand, although the existence of interrupted copulations prevented the estimation of the total number of copulations performed by females, the figures obtained could be good estimates of the number of copulations resulting in spermatophore transfer.

**Males transfer only one spermatophore per copulation.** In *C. xami* this is not true since in laboratory experiments we observed three copulations in which different males transferred two spermatophores during one copulation (Cordero 1998). Violation of this assumption results in an overestimation of copulation frequency.



However, if the frequency of copulations resulting in the transfer of two spermatophores in the laboratory is a good estimate of their frequency in the field (3/199 copulations observed in the laboratory), its quantitative effect should be small.

**Spermatophores always leave recognizable remains within the corpus bursae of the female.** This is not true in *C. xami* since in the laboratory it was not always possible to observe clear spermatophore remains in very old females that had laid most of their eggs (pers. obs.). However, judging from wing wear, no female in this condition was sampled (see paragraph four above).

In conclusion, the possible violation of the first and the last assumptions, and the fact that some of the females may have mated again had they not been collected, results in an underestimation of the frequency of copulations in females; whereas the fact that some males transfer more than one spermatophore in one copulation results in an overestimation of the number of copulations. However, judging from the low frequency of "interrupted" copulations (4.4%), very worn females in the field (at least during the sampling period), and copulations resulting in the transfer of two spermatophores (1.5%), I conclude that spermatophore counts are a reasonably good estimate of female copulation frequency in *C. xami*.

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#### ADDITIONAL NOTES ON *PROSERPINUS CLARKIAE* AND *ARCTONOTUS LUCIDUS* (SPHINGIDAE) LIFE HISTORIES FROM THE PACIFIC COAST OF NORTH AMERICA

**Additional key words:** Onagraceae, Rubiaceae, *Gayophytum*, *Galium*, *Clarkia breweri*, *Clarkia modesta*, *Camissonia*.

Host associations for *Proserpinus clarkiae* (Boisduval) and *Arctonotus lucidus* (Boisduval) have recently been documented. *Proserpinus clarkiae* was found using *Clarkia unguiculata* (Lindley) in nature (Osborne 1995). Here, I compare results of my life history work on *P. clarkiae* with other results (Hardy 1959) on this species. The life history of *A. lucidus* is also known (Comstock & Henne 1942). However, the first natural host associations for *A. lucidus* were made by photographs and collections from *Clarkia* species in California, and are presented here along with observations on captive rearing of this moth. The immature stages of these related sphingid species have been confused in the field by some, possibly due to their sympatry, common use of *Clarkia* hosts, and superficial resemblance. Thus, I will also discuss morphological differences among these and other sympatric *Clarkia* feeding sphingids.

In presenting the biology of *P. clarkiae* (Osborne 1995), I repeated the assertion made by Hodges (1971) that its life history was unknown. Since that time, Dr. Frederick Rindge (American Museum of Natural History) has drawn my attention to a life history of *P. clarkiae* that predates both works. Larvae and a pupa reared from Vancouver Island (Hardy 1959) were described by Hardy (1959), and match the immatures of *P. clarkiae* from California. Hardy obtained seven ova by confining females over potted *Galium aparine* (Lewis & Szwedkowski) (Rubiaceae). He reared at least one individual to pupation on that plant, but a field host was not given. The single fifth instar larva of *P. clarkiae* from Vancouver Island had the lateral dark blotches contiguous in an undulating line, a trait consistent

with some (< 5%) of the California material I reared (most California larvae had oblique blotches disjunct) (Osborne 1995). This dark form may be typical of cool, wet, north coastal localities, where darker maculation may impart local selective advantages, or may be an artifact of captive rearing.

Dr. Robert Raguso, who studied sphingid pollination of *Clarkia* species in central California (see Raguso & Pichersky 1995, Raguso et al. 1996, Raguso & Light 1998), sent me several suspected *Proserpinus* larvae, a reared pupa, and a photograph (Fig. 1) of a fifth instar larva in nature on *Clarkia breweri* (A. Gray) E. Greene. These specimens were all collected from *C. breweri* and *Clarkia modesta* (Jepson) at Del Puerto Canyon, Stanislaus Co., California in May, 1991. However, instead of *P. clarkiae*, all were determined (by KHO) to be *Arctonotus lucidus*, a closely related species from a monotypic genus. Early instar *A. lucidus* larvae may be separated from *P. clarkiae* by the presence of a black anal horn which is absent in *P. clarkiae*. Fifth instar *A. lucidus* lose the anal horn, but have dorsal and lateral markings of olive green (but briefly black just after molt [Comstock & Henne 1942]), not black or gray as in *P. clarkiae*. In addition, *A. lucidus* can be distinguished from *P. clarkiae* on the basis of dorsal, transverse intersegmental lines of tan or cream breaking the olive green field, and ventral whitish or gray. The ground color in fifth instar *A. lucidus* larvae is variable (Comstock & Henne 1942), ranging from black to olivaceous green to light green, to pink (Comstock & Henne 1942; D. Rubinoff pers. comm.; K. H. Osborne unpubl. obs.).





FIG. 1. Fifth instar *Arctonotus lucidus* larva on *Clarkia breweri* at Del Puerto Canyon, Stanislaus Co. CA., May, 1991. Photograph by Robert Raguso.

Raguso's photograph of an *A. lucidus* larva on *C. breweri*, and collections of *A. lucidus* from *C. breweri* and *C. modesta*, represent the first natural host records for this moth. Raguso (pers. comm. 1995) has seen [these?] larvae on *Clarkia gracilis sonomensis* (Hitchc.) near Lake Berryessa, Napa Co., California. (These records must be considered as likely *A. lucidus* but could possibly be *P. clarkiae*). Additionally, one wandering fifth instar *A. lucidus* (determined by KHO) was found by M. Lynn (pers. comm.) in May, 1997 in the immediate vicinity of abundant *Camissonia bistorta* (Nutt.), *Camissonia strigulosa* (Fisk. & Meyer) Raven [= *Oenothera contorta* Munz], and *Clarkia purpurea* (Curt.) Nels. & Macbr. at Lake Skinner, Riverside Co., California, suggesting these plants as possible hosts. The *Camissonia* species are used as larval hosts by related sphingids in southern California, *Euproserpinus phaeton* Grote & Robinson using *C. bistorta* (Osborne 1995), *Euproserpinus euterpe* Hy. Edwards using *C. strigulosa* (Tuskes & Emmel 1981, K. H. Osborne unpubl. obs.), and *Hyles lineata* (L.) using both (K. H. Osborne unpubl. obs.). *Clarkia breweri* is restricted to central California from Alameda Co. south to Fresno Co. (Munz 1959) and *C. modesta* ranges through California from Tehama Co. south to Santa Barbara Co. (Hickman 1993). The wide range of *A. lucidus* (Holland 1903, Hodges 1971) from British Columbia at least as far south as San Diego Co., California (Brown & Donahue 1989; Osborne unpubl. obs.) indicates *A. lucidus* must use other host plant species.

*Galium*, suitable for *P. clarkiae* in captivity (Hardy 1959), was rejected by *A. lucidus* as were two unnamed *Oenothera* species (Comstock & Henne 1942). In captivity, *A. lucidus* larvae would accept leaves of *C. breweri*, *C. modesta* and *Clarkia affinis* (H. Lewis & M. Lewis) (Raguso pers. comm.), but were hesitant to accept *Clarkia*

*unguiculata* (Lindley) and *Fuchsia* (K. H. Osborne unpubl. obs.; Raguso pers. comm.). Most prepupal *A. lucidus* larvae wandered and died without pupating in dry, sandy soil, and the one that did pupate, about 3 cm below ground in loose gravel, was attacked by mold and never emerged (K. H. Osborne unpubl. obs.; Raguso pers. comm.). Dan Rubinoff (pers. comm.) reported success getting *A. lucidus* to pupate on moist potting soil and when reared by Comstock & Henne (1942) larvae pupated as deep in the soil as possible (in cages).

*Hyles lineata* is common on *Clarkia* (*C. unguiculata* at Gates Canyon, Solano Co, CA [unpublished records] and *C. breweri*, at Del Puerto Canyon [Raguso]) when *A. lucidus* and *P. clarkiae* may be present. *Hyles lineata* is easily distinguished from larvae of *A. lucidus* and *P. clarkiae* by its prominent orange or yellow anal horn in all larval stages and by distinctive (but variable) longitudinal markings (Hodges 1971).

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